

A PRELIMINARY REVISION OF THE
INDO-PACIFIC ALOSINAE
(PISCES: CLUPEIDAE)



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ABSTRACT

Hilsa Regan and *Gudusia* Fowler are the only two Indo-Pacific genera of the clupeid sub-family Alosinae. New systematic characters are examined and the genus *Hilsa* is divided into the subgenera *Hilsa* (*H. kelee*) and *Tenualosa* (*H. ilisha*, *H. reevesii*, *H. macrura* and *H. toli*). *Macrura* van Hasselt is not a senior synonym of *Hilsa*. Two species of *Gudusia* are recognized (*G. chapra* and *G. variegata*).

The position of the West African genus *Ethmalosa* Regan is examined ; on present evidence, *Ethmalosa* is considered intermediate between the Indo-Pacific and the Atlantic Alosinae.

INTRODUCTION

The last revision of the Indo-Pacific Alosinae was that of Regan (1917), although Fowler (1941) listed all Indo-Pacific species and gave extensive synonymies. The more important species, such as *Hilsa ilisha*, have been fairly well studied, but others are little known and are poorly represented in museum collections. The material available has, however, enabled me to correct certain errors in previous synonymies and, using characters not employed before, to define the species more precisely. At the same time these characters have renewed the problem of the true phyletic relationships, both within the Indo-Pacific group, and between them and the Eastern Atlantic and New World groups. Such features as the development of a cleithral lobe or the presence of a striated fronto-parietal wedge appear in clupeid genera which otherwise are not closely related, and until the significance of such

characters within the whole family can be reviewed, their importance relative to other characters within the Alosinae can only be guessed at. For this reason, and also because of the lack of specimens in some species, this study can represent no more than a preliminary revision.

Regan (*loc. cit.*) treated as a single group those clupeid genera which have a distinct notch in the middle of the upper jaws, stating that "all these fishes appear either to be migratory, entering rivers to spawn in fresh or brackish water, or are permanently fluviatile." Regan then divided this group into those genera in which the epibranchial gillrakers near the angle of the arch fold down over the gillrakers of the ceratobranchial; and those in which the gillrakers near the angle of the arch lie roughly in the same plane. In the first section he placed the genera *Alosa*, *Caspialosa*, *Brevoortia*, *Pomolobus* and *Ethmidium*; and in the second section he placed the gizzard shads and the genera *Hilsa*, *Gudusia* and *Ethmalosa*. Svetovidov (1952) placed all these genera in the subfamily Alosinae, except the gizzard shads, which he removed to a separate subfamily, the Dorosomatinae.

Regan's gillraker character would seem to be a useful means of dividing the Alosinae into two tribes. It is supported by a difference in pelvic finray number, the Indo-Pacific genera having 8 rays, and the New World, Eastern Atlantic and Mediterranean genera having 7 or 9. However, the West African genus *Ethmalosa* appears to be as closely allied to the Atlantic Alosinae as it is to those of the Indo-Pacific. This is discussed in more detail later.

Both *Hilsa* and *Gudusia* contribute to important fisheries, and in Bengal, *Hilsa ilisha* is the most popular of all marine fishes (Hora 1954). The *Hilsa ilisha* fisheries of India have received considerable attention among Indian workers, and much of the available biological knowledge has been summarised by Pillay and Rosa (1957). *H. ilisha*, and probably all other species, is anadromous, but land-locked populations exist (e.g. in Chilka Lake—see Mitra and Devasandarum 1954). *Gudusia* on the other hand is purely fluviatile. *Hilsa* has a wide distribution, from Natal to China, but *Gudusia* is restricted to the rivers of India and Burma.

Regan (*loc. cit.*) used the form of the fronto-parietal ridges to divide his seven species of *Hilsa* into two groups. I have here followed Fowler (1934, 1941) in using this character to support a subgeneric division within *Hilsa*. Further characters are discussed which reinforce such a division.

The following classification has been adopted here :—

Subfamily Alosinae (Shads)

Genus *Hilsa*

Subgenus *Hilsa* (*H. kelee*)

Subgenus *Tenualosa* (*H. ilisha*, *H. reevesii*, *H. toli*, *H. macrura*)

Genus *Gudusia* (*G. chapra*, *G. variegata*)

Note on measurements used.

LENGTH : standard length used throughout.

HEAD LENGTH : the longest measurement, from premaxillary symphysis to posterior border of suboperculum, occasionally to posterior border of operculum.

MAXILLA LENGTH : from premaxillary symphysis to maxilla tip.

PREORBITAL DISTANCE : this measurement *includes* the eye, i.e. premaxillary symphysis to posterior border of eye.

CAUDAL LENGTH : length of unscaled portion of lower lobe.

SYSTEMATIC CHARACTERS

(a) *Fronto-parietal ridges.*

The two forms of fronto-parietal ridge found in *Hilsa* are shown in Figure 1A and B. In the *Hilsa* form (1A) the wedge-shaped ridges are exposed and bear numerous longitudinal striae. In the median area between the two wedges, the frontals are covered by a thin layer of skin. The supra-occipital is exposed for some distance anteriorly, between the posterior tips of the frontals ; posteriorly it is raised into a median, transverse ridge.

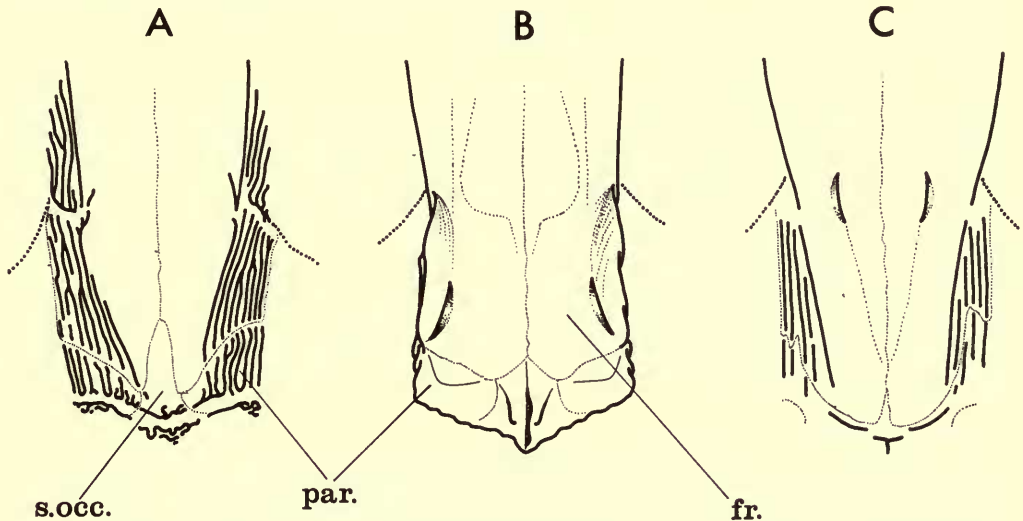


FIG. 1. Fronto-parietal striation patterns (dorsal view of posterior part of head, skin removed). A. "*Hilsa*" pattern (180 mm. fish, syntype of *Clupea durbanensis* = *H. kelee*). B. "*Tenuialosa*" pattern (210 mm. fish, *H. ilisha*). C. "*Gudusia*" pattern (150 mm. fish, *G. variegata*).

s. occ. supra-occipital. par. parietal. fr. frontal.

In the *Tenuialosa* form (1B) there is no wedge-shaped striated fronto-parietal ridge, although the lateral margins of the frontals in this area may form one or two longitudinal grooves. The entire region is covered by a thick layer of skin, but the lateral margins of the frontals are sometimes visible. The supra-occipital is partly exposed anteriorly, as in the *Hilsa* form ; posteriorly it bears a longitudinal ridge, flanked by two smaller longitudinal ridges.

In *Gudusia* (Figure 1C) the fronto-parietal ridges are striated and exposed and resemble those of the *Hilsa* form. However, the striae are not continued forward along the frontals to the same extent as in the *Hilsa* form.

The difference between the two subgenera of *Hilsa* in fronto-parietal ridge form is in fact greater than that which separates the clupeid genus *Sardinella* from either *Harengula* (Western Atlantic) or *Herklotsichthys* (Indo-Pacific). In these genera the fronto-parietal character appears to hold genuine phyletic significance (Whitehead, 1964a), and it is therefore possible that the two groups of *Hilsa* might be more correctly allocated to separate genera also. For the time being, however, and until this character can be studied in other clupeid genera, I have preferred to maintain a subgeneric division only.

(b) *Maxillary bones*

In the genus *Hilsa* there are two supra-maxillae lying along the dorsal margin of the maxilla. The second or posterior supra-maxilla is expanded and paddle-shaped posteriorly and pointed and shaft-like anteriorly. There is some variation in the shape of the expanded portion (smaller than in other species in *H. ilisha* and *H. reevesii*), but there is no trenchant difference in size or shape between the two subgenera. The first or anterior supra-maxilla, however, is slightly deeper in *Hilsa* (*Hilsa*) than in *Hilsa* (*Tenualosa*).

The expanded (posterior) portion of the maxilla is similar in general shape in both subgenera, but is rather longer in *H. ilisha* and *H. reevesii*. In the subgenus *Hilsa* (*Hilsa*), however, there are four to six longitudinal ridges on this expanded portion (Figure 2A), but these are absent in *Hilsa* (*Tenualosa*) (Figure 2B and C). Occasionally species of the latter subgenus may have one or more fine grooves in the maxilla, but these are never developed into ridges.

H. macrura has a much shorter maxilla than have other species (Figure 2B), the tip not passing the vertical through the pupil of the eye.

In *Gudusia* the maxilla and supra-maxillae closely resemble those of *Hilsa* (*Tenualosa*), especially *H. (T.) toli*.

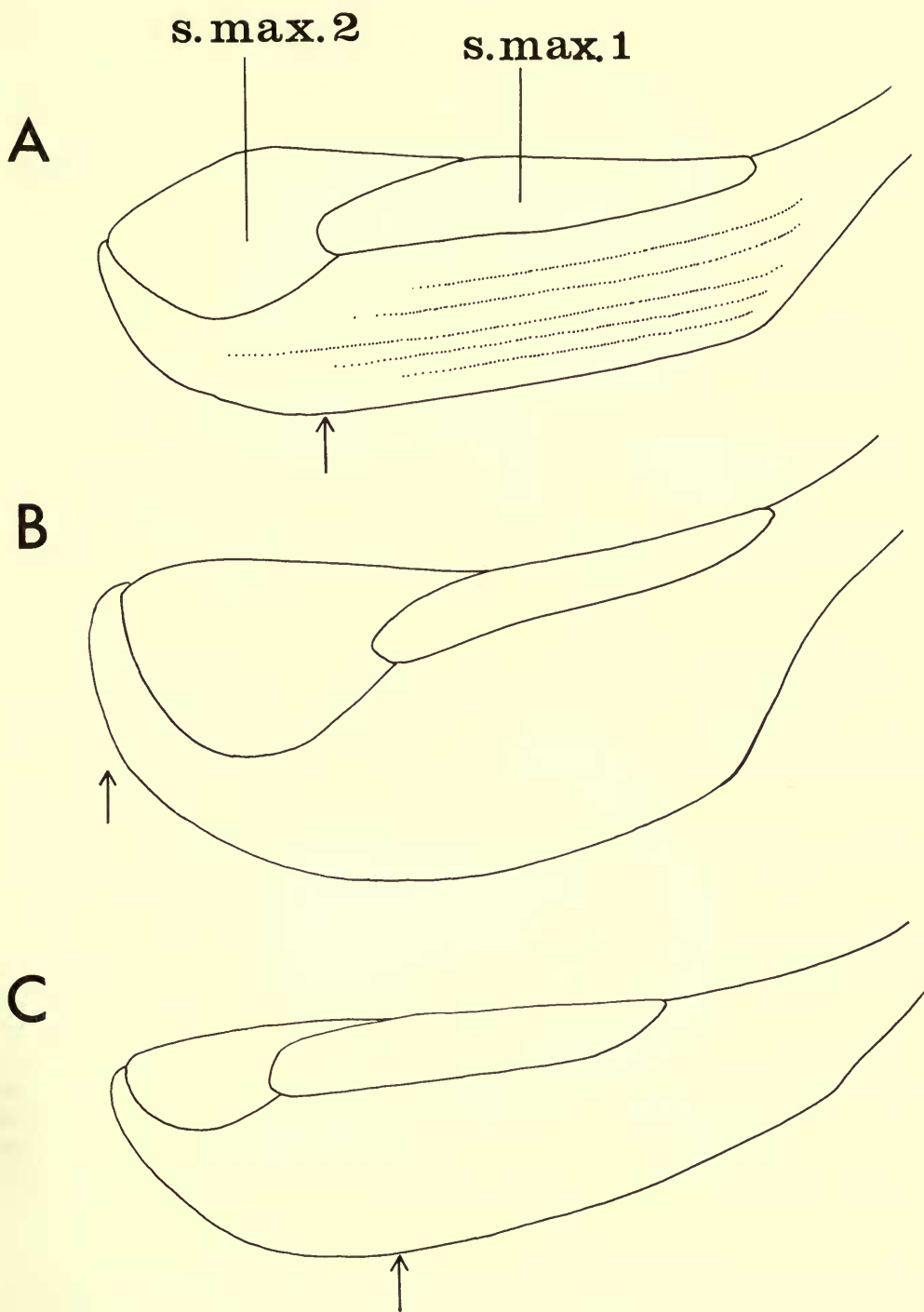
(c) *Cleithral lobe.*

In clupeid fishes the tissue covering the anterior margin of the cleithrum may be expanded in places, thus giving the gill cavity an irregular posterior outline. In some genera, for example in *Sardinella*, there is a fleshy lobe at the postero-ventral angle of the gill opening, just above the base of the pectoral fin. This lobe, which occurs in some genera of the Dussumieriidae, I have elsewhere termed the cleithral 'flap' (Whitehead, 1963), but 'lobe' is perhaps a better term.

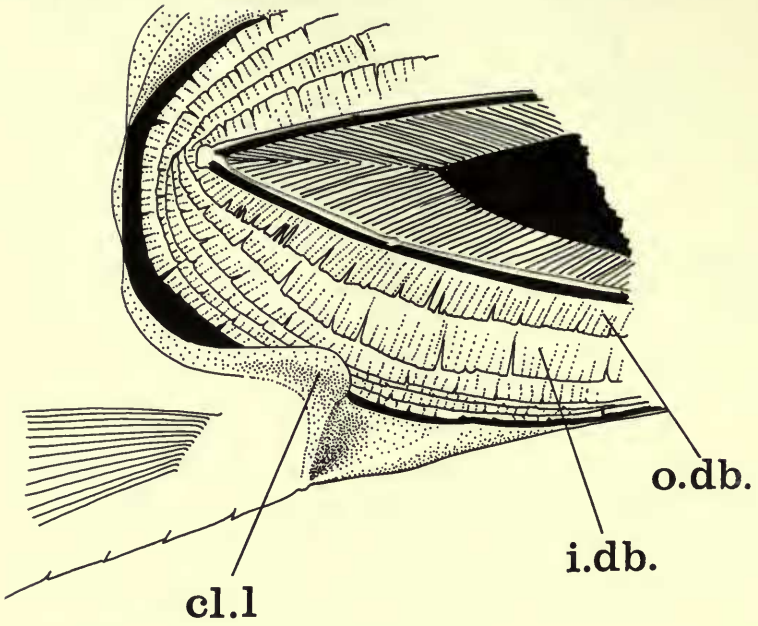
In the subgenus *Hilsa*, the cleithral lobe is well developed, breaking the posterior outline of the gill opening and projecting sufficiently to cover the underlying filaments of all but the first gill arch (Figure 3A). In front of the cleithral lobe there is an oblique groove. The final two branchiostegal rays cover this groove.

In species of the subgenus *Tenualosa*, the cleithral lobe projects little into the gill cavity and in most cases barely interrupts the cleithral outline (Figure 3B). In

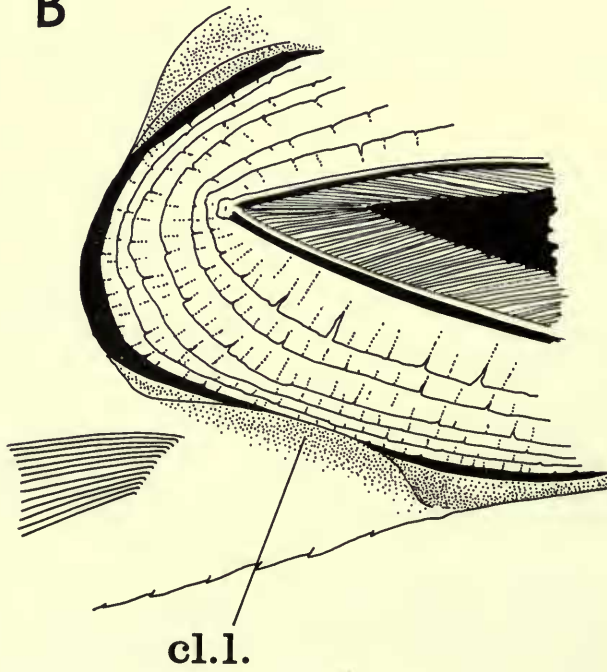
FIG. 2. Maxillary bones in species of *Hilsa* (right side). Arrow indicates vertical through eye centre. A. *Hilsa kelee* (syntype of *Clupea durbanensis*, 180 mm.). B. *Hilsa macrura* (160 mm. specimen, Sarawak). C. *Hilsa ilisha* (210 mm. specimen, Calcutta).
s. max. 1 anterior supra-maxilla. s. max. 2 posterior supra-maxilla.



A



B



H. macrura the cleithral lobe is rather more developed, but it never projects into the gill chamber to the same extent as in *H. kelee*. In *H. macrura* and other species of *Hilsa* (*Tenuulosa*) the groove in front of the cleithral lobe is either very shallow or absent.

This character is less apparent in juvenile fishes, and in small specimens of *Hilsa* (of about 50 mm.) the cleithral lobe is similar and poorly developed in both subgenera.

In *Gudusia* the cleithral lobe is slightly developed, and resembles that of *H. macrura*, i.e. it is intermediate in size between *Hilsa* (*Hilsa*) and *Hilsa* (*Tenuulosa*).

(d) *Gill filaments.*

In the subgenus *Hilsa*, the gill filaments of the outer hemibranch of the first gill arch are very short, barely half the length of those of the inner hemibranch. In species of *Hilsa* (*Tenuulosa*), the filaments of the outer hemibranch are more than a half the length of those of the inner hemibranch (Figure 3A and B).

In juveniles, the outer filaments in species of *Hilsa* (*Tenuulosa*), tend to be relatively shorter, but the distinction between the two subgenera is normally obvious, and especially if comparative material is available.

Gudusia resembles *Hilsa* (*Tenuulosa*), having the filaments of the outer hemibranch more than half the length of those of the inner hemibranch.

(e) *Gillrakers.*

In the subgenus *Hilsa*, the gillrakers on the second, third and fourth arches are curled outwards (Figure 4B). At the tip of the raker there is a small knob which, *in situ*, rests against that of its neighbours so that the raker tips are held in line. The inner (convex) margin of each raker bears a series of short spines or serrae (about 100 on each raker). Along the outer margin (concave) there is a thin flange of skin, expanded on some rakers, narrow on others.

The lower gillrakers of the first arch in the subgenus *Hilsa* are longer than the corresponding gill filaments, and in fishes over 80 mm. standard length they exceed eye diameter (three-quarter eye diameter at 50 mm.).

In the subgenus *Tenuulosa* the gillrakers on all arches are straight or very slightly curved (Figure 4A). The serrae are slightly fewer than in *Hilsa* and there is no flange of skin along the outer margin of the raker. The tips of the rakers are pointed, except in *H. macrura*.

The lower gillrakers of the first arch in *Hilsa* (*Tenuulosa*) are as long as those in *Hilsa* (*Hilsa*) except in the case of *H. macrura* (Figure 4C), where they are about half the length of the corresponding gill filaments (less than the diameter of the pupil at 150 mm. standard length).

In *Gudusia* the gillrakers are straight or slightly curved and resemble those of *H. ilisha* in form and length.

FIG. 3. Cleithral profile and gill arches (right side, operculum removed). A. *Hilsa kelee* (syntype of *Clupea durbanensis*, 180 mm.). B. *Hilsa ilisha* (210 mm. specimen, Calcutta). cl. l. cleithral lobe. o. db. outer hemibranch of 1st arch. i. db. inner hemibranch of 1st arch.

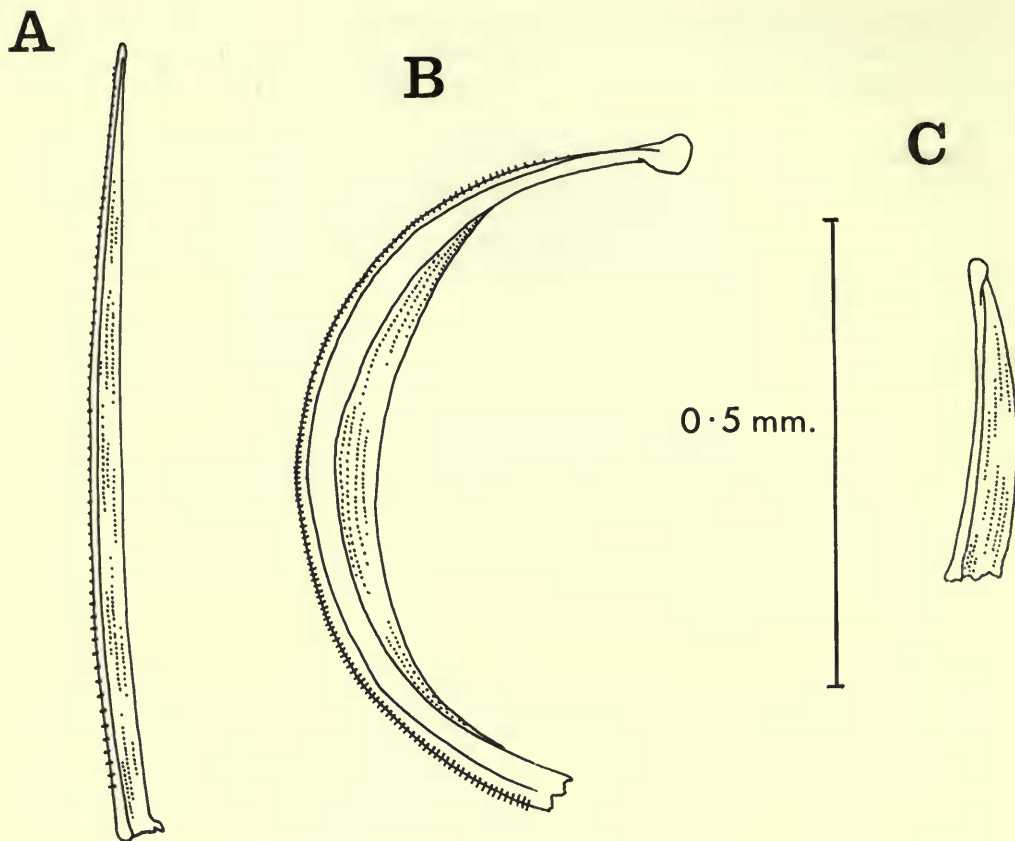


FIG. 4. Gillrakers from lower part of first arch in species of *Hilsa*. A. *Hilsa ilisha* (215 mm. fish). B. *Hilsa kelee* (syntype of *Clupea durbanensis*, 180 mm.). C. *Hilsa macrura* (155 mm. fish).

(f) *Opercular bones.*

In *Gudusia* the lower margin of the operculum rises more steeply than in either *Hilsa* (*Hilsa*) or *Hilsa* (*Tenuulosa*) (Figure 5A and B). If the line of the lower operculum margin is produced posteriorly, it intersects the dorsal body profile near or in front of the dorsal origin in *Gudusia*, but behind this point in *Hilsa*. In *Gudusia* the suboperculum is in consequence less rectangular.

Within *Hilsa* (*Tenuulosa*) there is some variation in the shape of the operculum and suboperculum. In *H. macrura* the latter is almost rectangular and the lower border of the operculum is near the horizontal. *H. toli* and *H. ilisha* resemble *H. kelee* (Figure 5A). In *H. reevesii* the operculum and suboperculum are broader than in other species, the length of the suboperculum (upper exposed margin) being contained less than twice in the height of the operculum (more than twice in all other species of *Hilsa*, but not in *Gudusia*).

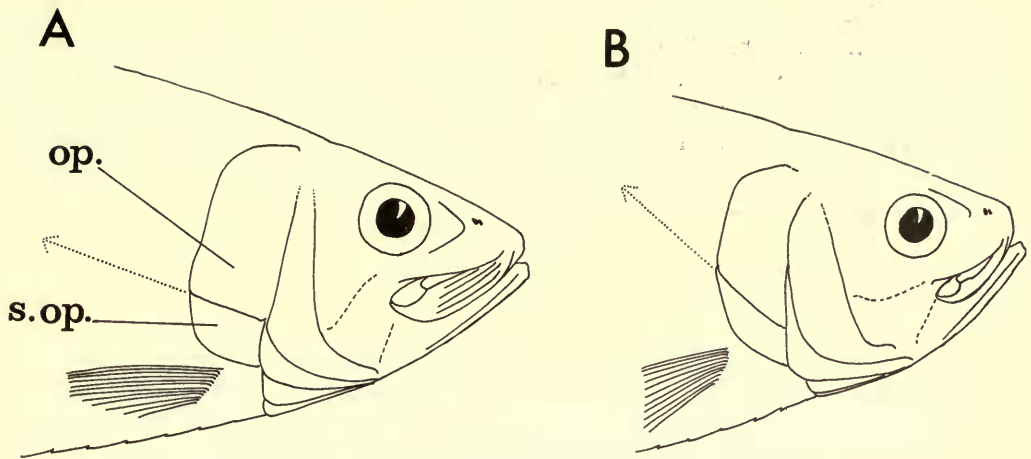


FIG. 5. Opercular bones in *Hilsa* and *Gudusia*. Dotted arrow indicates line projected along upper (exposed) margin of sub-operculum. A. *Hilsa kelee* (syntype of *H. durbanensis*, 180 mm.). B. *Gudusia variegata* (150 mm. fish).

op. operculum. s. op. sub-operculum.

(g) *Pseudobranchiae*.

Pseudobranchiae are present in all genera of the Alosinae. In *Hilsa* there are slight interspecific differences in the shape of the pseudobranch, and one of these is sufficiently marked to be commented on.

The pseudobranch in *H. ilisha* and *H. reevesii* differs from that of all other species of *Hilsa* in having a slightly longer base and a more attenuated appearance (Figure 6A). Although the longest pseudobranchial filaments are as long as those in other species, filament length decreases more gradually posteriorly (cf Figure 6A and B). The difference between these two forms is not great, but is easily apparent when a comparison can be made. In addition, *H. ilisha* and *H. reevesii* have a distinct groove below the base of the pseudobranch, into which the tips of the gillrakers of the first arch fit. A groove is absent in *H. toli* and *H. macrura*, but occurs in *H. kelee*.

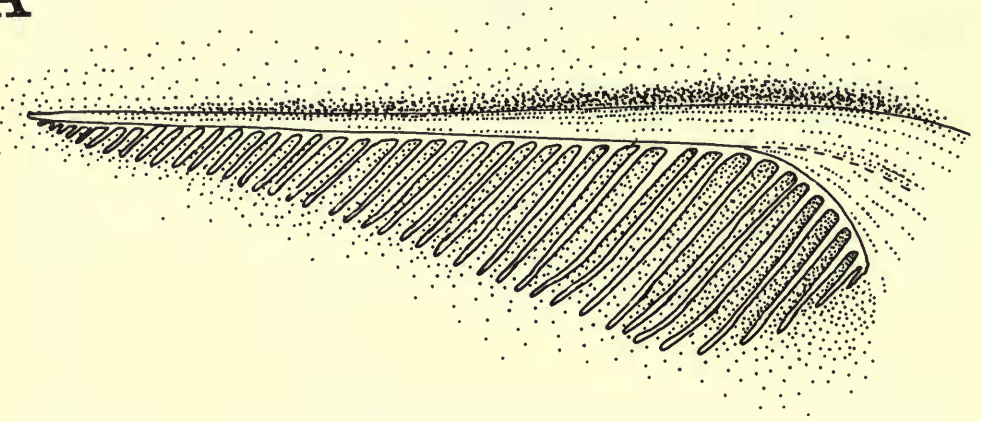
The pseudobranch in *Gudusia* is attenuated and resembles that of *H. ilisha*. A groove is present.

THE ALOSINAE OF THE INDO-PACIFIC

While *Hilsa kelee* is sufficiently distinct from the remaining species of *Hilsa* to be separated subgenerically (or even generically), *Gudusia* combines characters from both of the subgenera, but at the same time possesses its own distinctive features. The question arises whether the degree of affinity between the three taxa, *Hilsa* (*Hilsa*), *Hilsa* (*Tenualosia*) and *Gudusia*, is equal or whether one has diverged further from the other two. The distinctive characters of each are shown in Table I.

Hilsa (*Hilsa*) is distinguished from *Gudusia* on seven counts, and from *Hilsa* (*Tenuulosa*) on five, while the latter is distinguished from *Gudusia* on four counts. But obviously some characters have more phyletic importance than others. The fronto-parietal character links *Hilsa* (*Hilsa*) with *Gudusia*, but in other respects *Gudusia* would appear to have evolved as a fluviatile offshoot of *Hilsa* (*Tenuulosa*), the increase in scale number being linked with this change of habitat. If *Gudusia* is recognised as a separate genus, then there is good reason for separating *Hilsa*

A



B

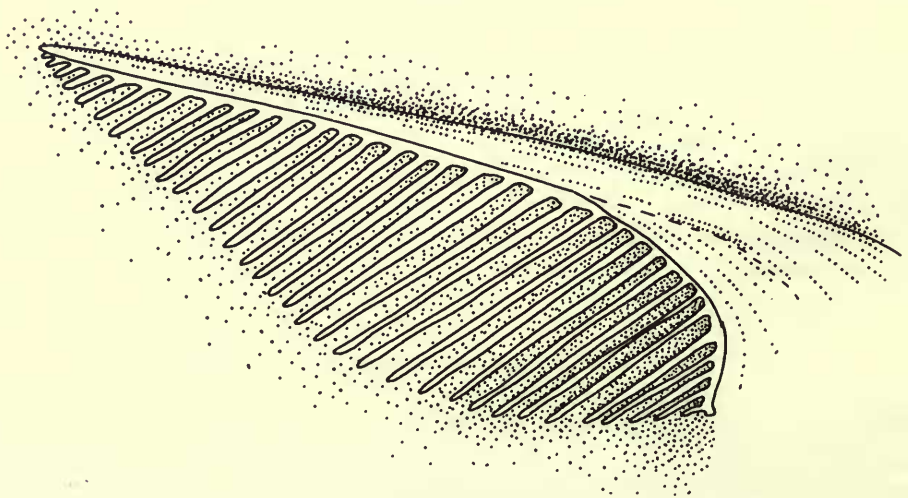


FIG. 6. Pseudobranch shape in species of *Hilsa* (right side, with thickened lower edge shown uppermost). A groove present along lower edge in both species. A. *Hilsa ilisha*. B. *Hilsa kelee*.

(*Tenualosa*) at generic level too. Alternatively, each of the three taxa might be accorded subgeneric rank. Much depends on the importance accorded to the development of the fronto-parietal sculpture. Under these circumstances, I have preferred to leave *Gudusia* as a separate genus and to retain the *Tenualosa* forms within *Hilsa* for the time being. Fowler (1958) proposed a new subfamily, the Gudusiinae, defined to include *Gudusia* alone, but this does not seem to be justified.

TABLE I

<i>Hilsa</i> (<i>Hilsa</i>)	<i>Hilsa</i> (<i>Tenualosa</i>)	<i>Gudusia</i>
Curled gillrakers.	No fronto-parietal striated wedge.	Small and numerous scales.
Large cleithral lobe.		Steeply rising operculum lower border.
Ridged maxilla.		Fluviatile habit
Short outer hemibranch on first arch.		

Diagnosis.

Indo-Pacific clupeid fishes with a distinct notch in the middle of the upper jaw and with the gillrakers of the epibranchial of the first arch not folding over those of the ceratobranchial. Gillrakers present on inner face of epibranchial of third arch. Pseudobranch present. Body compressed, with pre- and post-pelvic scutes, but no pre-dorsal scutes. Two supra-maxillae, the posterior one expanded; no hypomaxilla. Operculum smooth or with a few fine vertical striae. Anal fin moderate 18-29 rays, of which the last two are normal and not enlarged. Pelvic fins present, 8-rayed, not reduced in size; pelvic origin a little behind dorsal origin. No alar scales on caudal fin. Purely riverine (*Gudusia*) or marine and anadromous (*Hilsa*). From Natal to China.

KEY TO THE GENERA AND SUBGENERA

- I Scales large, 40-50 in lateral series; lower edge of operculum as in Figure 5A; marine, anadromous ***Hilsa* Regan**
 - a Fronto-parietal ridges exposed, bearing many longitudinal striae (Figure 1A); exposed part of expanded portion of maxilla with 4-6 longitudinal ridges (Figure 2A); cleithral lobe prominent (Figure 3A); gill filaments of outer hemibranch on first arch not more than half length of inner hemibranch; gillrakers on second, third and fourth arches curled outwards (Figure 4B) subgenus ***Hilsa***
 - b Fronto-parietal ridges covered by skin, a few or no striae present (Figure 1B); maxilla smooth on exposed part of expanded portion (Figure 2B); cleithral lobe not prominent (Figure 3B); gill filaments of outer hemibranch on first arch more than half length of those on inner hemibranch; gillrakers on second, third and fourth arches straight or very slightly curved (Figure 4A and c) subgenus ***Tenualosa***
- II Scales small, 80-120 in lateral series; lower edge of operculum steeply inclined as in Figure 5B; fluviatile. ***Gudusia* Fowler**

Hilsa Regan

Hilsa Regan, 1917, *Ann. Mag. nat. Hist.*, (8) **19** : 303 (type *Paralosa durbanensis* Regan, ex Durban).

Paralosa Regan, 1916, *Ann. Durban Mus.*, **1** (3) : 167 (type *Clupea durbanensis* Regan) (non Bleeker 1872, see below).

Tenualosa Fowler, 1934, *Proc. Acad. nat. Sci. Philad.*, **85** : 246 (type *Alosa reevesii* Richardson ex China).

Macrura Fowler, 1941, *Bull. U.S. nat. Mus.*, No. 100 : 626 (type *Clupea kelee* Cuvier) (see note on *Macrura* van Hasselt).

Indo-Pacific alosinid fishes with moderate scales, 40–50 in lateral series, 12–20 in transverse series ; scales adherent. Suboperculum rectangular, or subrectangular, its junction with the operculum, if produced, cutting the dorsal profile in the middle of the dorsal base or behind (Figure 5A).

Branchiostegal rays 5–6. Gillrakers numerous, 60–220, slender. Dorsal rays 17–20, pelvic 8, anal 17–22. Ventral scutes, 16–19 pre-pelvic and 11–15 post-pelvic.

Two subgenera and five species recognised here, from coasts and rivers from Natal to China.

Note on synonymy.

Fowler (1941) believed *Macrura* van Hasselt 1823 to be the earliest available generic name for those clupeid fishes related to the 'Keelee' of Russell (1803, p. 75, pl. 195), i.e. *kanagurta*, *ilisha*, *toli*, etc. Smith (1949, p. 90) followed Fowler's example, as also did Whitley (1948 and 1953) and Munro (1955). Indian workers, on the other hand, have generally placed these species in *Hilsa* Regan 1917. Regan (1916) proposed *Paralosa* for those Indo-Pacific species placed by Bleeker (1872) in *Alosa*. Later, (Regan 1917) he created *Hilsa* to replace his monotypic *Paralosa*, presumably on grounds of homonymy, although this is not stated ; *Paralosa* Bleeker 1872 is in fact a junior synonym of *Sardinella* (Whitehead 1964a). Since the works of Fowler, Smith and Whitley are quite extensively used, and since the original indication of *Macrura* by van Hasselt is not easy to locate, it is worth citing the relevant passage here.

Macrura is first mentioned in a letter from van Hasselt to Temminck published in the *Algemeene Konst- en Letter-Bode*, **1**, No. 20, 16th May, 1823, and titled "Uittreksel uit een' Brief van Dr. J. C. van Hasselt aan den Heer C. J. Temminck."

p. 329 "De Koelee (?) van Russ. Tab. 195 is hier in groote hoeveelheden, en hierbij voegt zich eene, welke ik heb doen afbeelden en den naam *Macrura* gegeven heb"*

The Koelee is the *Keelee* of Russell (1803). No figure accompanies the text (but see below, p. 142). The use of a capital initial letter for *Macrura* does not necessarily indicate a generic name, since capitals are occasionally, and for no apparent reason, used elsewhere in the text (*Clupea Melostoma* for example). A translation of this letter, published the following year (1824) in the *Bull. Sci. nat. geol.* (Ferussac), **2** : 89–92, confirms that *Macrura* was intended as a specific name.

*"The Koelee (?) of Russ. Plate 195 is here in large numbers, and to that must be added one which I have had figured and have given the name *Macrura*."

p.92 " Dans le genre *Clupea* Lin. mes collections sont plus riches ; j'ai divers individus du *Cl. melastoma* Schn., et l'espèce représentée par Russell, pl. 195, se trouve ici en quantité ; il faut y joindre une autre espèce que j'ai fait dessiner sous le nom de *macrura*."

Macrura van Hasselt should not, therefore, appear in the synonymy of *Hilsa*.

Subgenus *Hilsa*

As defined in key. A single species recognised here, *H. (Hilsa) kelee*.

Hilsa kelee (Cuvier)

- Clupea kelee* Cuvier, 1829, *Règne animal*, ed. 2, **2** : 320 (on *Keelee* Russell, 1803, *Fishes of Coromandel*, **2** : 75, pl. 195 upper figure : type locality, Vizagapatam).
- Macrura kelee* : Fowler, 1941, *Bull. U.S. nat. Mus.*, No. 100 : 627 ; Smith, 1949, *Sea Fishes S. Africa* : 90 ; Munro, 1955, *Mar. F-water fish. Ceylon* : 24 ; Fowler, 1956, *Fishes of the Red Sea* : 69 ; Fourmanoir, 1957, *Mem. Inst. Sci. Madagasc. Serv. océanogr.*, **1** : 8, fig. 1.
- ?*Clupeonia blochii* Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 353 (type locality, Tranquebar).
- Hilsa blochii* : Fowler, 1926, *J. Bombay nat. Hist. Soc.*, **30** (4) : 3 ; *Idem*, 1938, *List. Fish. Malaya* : 27.
- Alosa brevis* Bleeker, 1848, *J. Ind. Arch.*, **2** : 638 (type locality, Bima, Sumbawa Island) ; *Idem*, 1872, *Atlas Ichth. Ind. Néerland.*, **6** : 116.
- Hilsa brevis* : Fowler, 1928, *Mem. Bishop Mus.*, **10** : 30.
- Macrura brevis* : Munro, 1958, *Papua New Guinea agric. J.*, **10** (4) : 116.
- Alausa kanagurta* Bleeker, 1852, *Verh. Bat. Gen.*, **24** : 13, 34 (type locality, Batavia, Muntok, East Indies) ; *Idem*, 1865, *Ned. Tijdschr. Dierk.*, **2** : 35, 176.
- Alosa kanagurta* : Bleeker, 1872, *Atlas Ichth. Ind. Néerland.*, **6** : 114, pl. 265, fig. 5 ; Bean & Weed, 1912, *Proc. U.S. nat. Mus.*, **42** : 590 ; Hora, 1924, *Mem. Asiatic Soc. Bengal*, **6** : 480 ; Suvatti, 1937, *Index Fish. Siam* : 9.
- Clupea kanagurta* : Day, 1878, *Fishes of India*, pt. 4 : 640, pl. 162, fig. 4 ; *Idem*, 1889, *Fauna British India, Fishes*, **1** : 377 ; Pillay, 1929, *J. Bombay nat. Hist. Soc.*, **32** (2) : 355 ; Tirant, 1929, *Serv. océanogr. Pêches Indochine*, 6^e note : 118, 120 ; Hardenberg, 1931, *Treubia*, **13** (1) : 111.
- Clupea (Alosa) kanagurta* : Weber & de Beaufort, 1913, *Fishes Indo-Aust. Archipelago*, **2** : 67 ; Chabanaud, 1926, *Serv. océanogr. Pêches Indo-Chine*, 1^e note : 8.
- Hilsa kanagurta* : Regan, 1917, *Ann. Mag. nat. Hist.*, (8) **19** : 304 ; Fowler, 1934, *Proc. Acad. nat. Sci. Philad.*, **86** : 86 ; *Idem*, *op. cit.*, **87** : 90, fig. 8 ; Suvatti, 1937, *Index Fish. Siam* : 12 ; Fowler, 1938, *List Fish. Malaya* : 27 ; Bertin, 1940, *Bull. Mus. Hist. nat. Paris*, (2) **12** : 281 (Bleeker cotype) ; Blegvad, 1944, *Danish Sci. Invest. Iran*, pt. 3 : 63 ; Misra, 1947, *Rec. Ind. Mus.*, **45** (4) : 390 ; Quereshi, 1957, *Agric. Pakistan*, **8** (2) : 107.
- Hilsa kanagurta* : Chu, 1931, *Biol. Bull. St. John's Univ.*, **1** : 14 (misspelt).
- Harengula kanagurta* : Paradise & Whitley, 1927, *Mem. Queensland Mus.*, **9** : 76, pl. 12, fig. 1 ; McCulloch, 1929, *Aust. Mus. Mem.*, **5** : 39 ; ?Wu, 1929, *Contr. Biol. Lab. Sci. Soc. China*, **5** (4) : 17, fig. 13 (see note on distribution, below).
- Alausa ilisha* : (non Hamilton-Buchanan) Bleeker, 1852, *Verh. Bat. Gen.*, **24** : 33 ; Kner, 1865, *Reise Novarra, Fische* : 331.
- Clupea ilisha* : Günther (part), 1868, *Cat. Fish. Brit. Mus.*, **7** : 445 ; Day (part), 1878, *Fishes of India*, pt. 4 : 640 ; *Idem* (part), 1889, *Fauna Brit. India*, **1** : 376.
- Alausa brachysoma* Bleeker, 1853, *Nat. Tijdschr. Ned. Ind.*, **5** : 527 (type locality, Padang, Sumatra) (non *Sardinella brachysoma* Bleeker).
- Alosa brachysoma* : Bleeker, 1872, *Atlas Ichth. Ind. Néerland.*, **6** : 115, pl. 262, fig. 5.
- Hilsa brachysoma* : Regan, 1917, *Ann. Mag. nat. Hist.*, (8) **19** : 305.

- Alosa chapra* : Günther, 1866, *Fishes of Zanzibar* : 123.
Alosa malayana Bleeker, 1866, *Ned. Tijdschr. Dierk.*, **3** : 294 (type locality, Java, Sumatra) ;
 Idem, 1872, *Atlas Ichthy. Ind. Néerland.*, **6** : 114, pl. 265, fig. 4.
Clupea platygaster Günther, 1868, *Cat. Fish. Brit. Mus.*, **7** : 448 (on Bleeker's Sumatra specimen
 of *Alausa brachysoma* in British Museum) ; Regan, 1914, *Trans. zool. Soc. London*, **20** (6) : 276.
Clupea (Alosa) platygaster : Weber & de Beaufort, 1913, *Fishes Indo-Austr. Archipelago*, **2** :
 66, fig. 24 ; Chevey, 1932, *Inst. océanogr. Indochine*, 19^e note : 9.
Alosa platygaster : Roxas & Martin, 1937, *Dept. Agric. Comm. Manila Tech. Bull.*, **6** : 21 ;
 Herre, 1953, *List. Philipp. Fishes* : 71.
Clupea durbanensis Regan, 1906, *Ann. Natal Gov. Mus.*, **1** (4) : 4, pl. 4 (type locality, Durban
 Bay) ; Idem, 1908, *op. cit.*, **1** (3) : 242 ; Gilchrist & Thompson, 1908, *Ann. S. Afr. Mus.*,
6 : 268 ; Gilchrist, 1913, *Marine Biol. Rep. S. Africa*, No. 1 : 59.
Paralosa durbanensis : Regan, 1916, *Ann. Durban Mus.*, **1** : 167 ; Gilchrist & Thompson,
 1917, *Ann. Durban Mus.*, **1** (4) : 297.
Hilsa durbanensis : Regan, 1917, *Ann. Mag. nat. Hist.*, (8) **19** : 305 ; Barnard, 1925, *Ann.*
S. Afr. Mus., **21** (1) : 111 ; Fowler, 1925, *Proc. Acad. nat. Sci. Philad.*, **77** : 195 ; Barnard,
Ann. S. Afr. Mus., **21** (2) : 1017 ; Fowler, 1934, *Proc. Acad. nat. Sci. Philad.*, **86** : 411 ;
 Idem, 1935, *op. cit.*, **87** : 365.

Note on synonymy.

Following Regan (1917), many modern authors have either doubtfully cited or ignored *Clupea kelee* Cuvier, 1829 (name without description in footnote, p. 320 in 2nd edition), but Fowler (1941) and Smith (1949) give Cuvier's name priority over *kanagurta* Bleeker. Cuvier states, however, that his *C. kelee* is based on Russell's figure of *Keelee*. Cuvier's name is thus a valid indication, being "a bibliographic reference to a previously published description, definition or figure" (Art. 16 (a), International Code of Zoological Nomenclature 1961).

Günther (1868, p. 445) included *Alausa toli* Cantor in his synonymy of *Clupea ilisha*. The smaller of the two Cantor specimens listed by Günther is *H. kelee* ; the larger is probably *H. toli* (but see p. 135). The remaining specimens listed by Günther under *Clupea ilisha* are *H. kelee*.

Alosa malayana Bleeker, as Weber and de Beaufort (1913) point out, seems to have been based on a juvenile specimen of *H. kelee*. Since eye diameter shows negative allometry with standard length, the maxilla appears to be shorter in smaller fishes, barely reaching to eye centre.

I have followed Fowler (1941) and Day (1878) in placing *Clupeonia blochii* Valenciennes in this synonymy, but have done so tentatively since Valenciennes based his description on the doubtful *Clupea sinensis* Bloch (see notes on the synonymy of *H. toli*).

Fowler (1941) followed Regan (1917) in separating *H. durbanensis* and *H. brachysoma* from *H. kelee*, distinguishing the first by its shorter head, and the second by its deeper body. In Figure 7A and B, head length and body depth are plotted (as percentages of standard length) for the specimens listed under Study Material. The figure shows that there is considerable variation (possibly sexual) in body depth, but that this cannot be ascribed to regional variation. In head length, the Durban specimens (i.e. *H. durbanensis*) have shorter heads than do the Gulf of Aden fishes, but the remaining Indian Ocean specimens are intermediate. On the basis of head length, the Gulf of Aden fishes might be recognised as distinct, but in all other

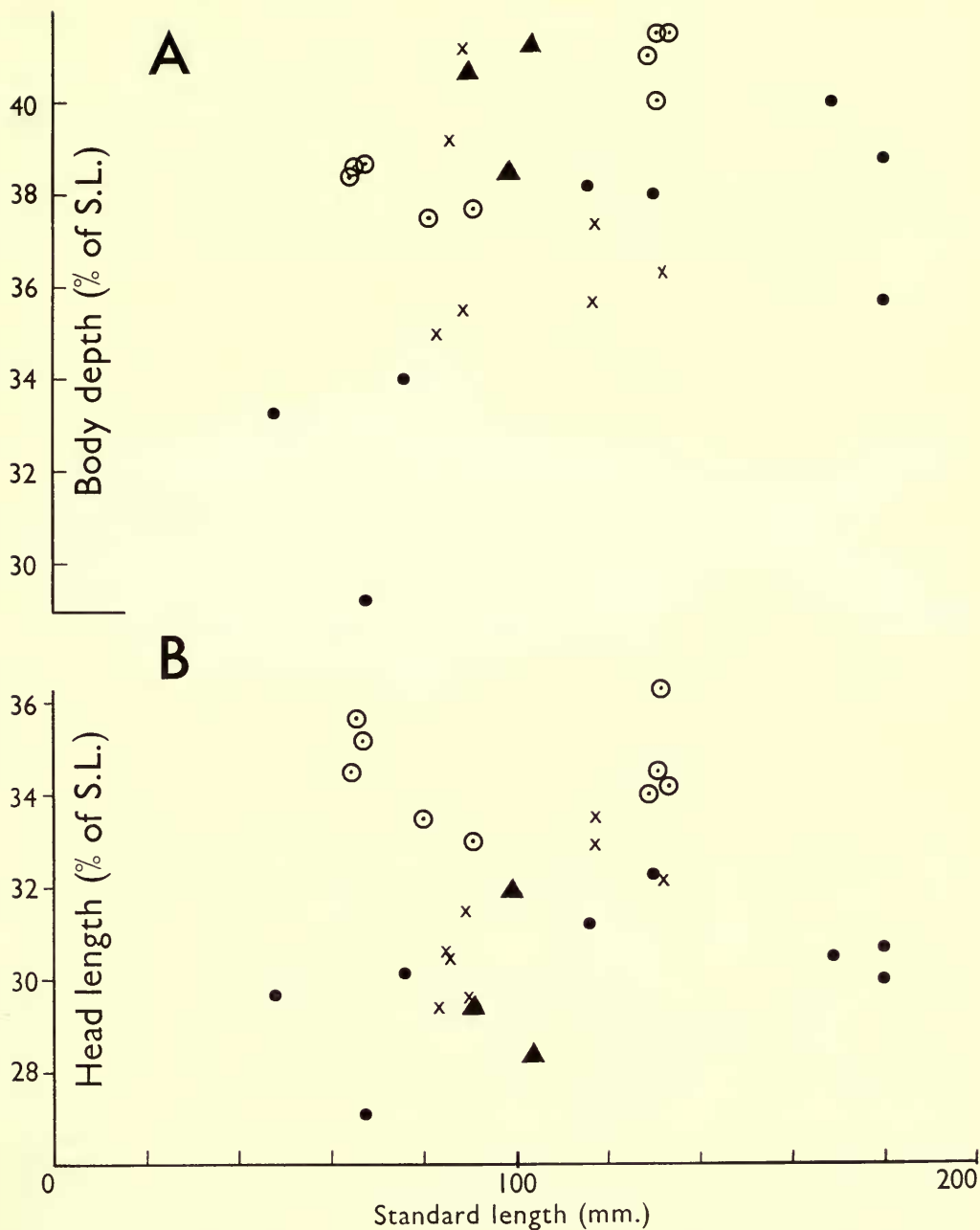


FIG. 7. Body depth (A) and head length (B) as percentages of standard length, plotted against standard length for specimens of *Hilsa kelee*. ● Durban, Kenya coast, Zanzibar. ○ Gulf of Aden. × East Indies. ▲ India.

morphometric and meristic measurements they are inseparable from the rest. I have found no other means of distinguishing *H. durbanensis* and *H. brachysoma*, and therefore recognise a single Indo-Pacific member of the subgenus *Hilsa*.

DESCRIPTION. Based on 24 specimens over 50 mm. listed under Study Material.

In percentages of standard length : body depth (29.2) 33.3-41.5 (Figure 7A), head length 27.1-36.3 (Figure 7B) ; snout length (5.7) 6.4-8.5 ; eye diameter 7.2-9.5, maxilla length 12.0-16.4 ; operculum, height 15.9-20.6, width 6.9-10.0 ; pectoral length 17.8-21.0, pelvic length 10.3-12.1, anal base 16.7-17.5 ; pre-dorsal 41.7-50.5, pre-pelvic 49.8-57.5.

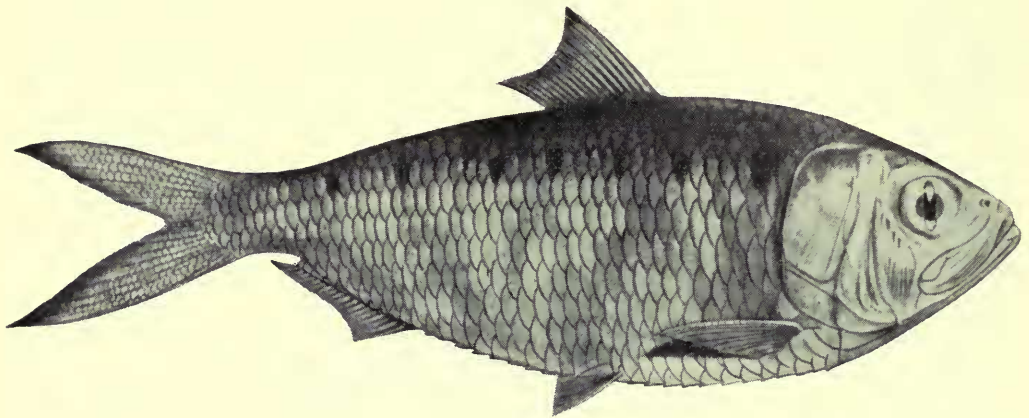


FIG. 8. *Hilsa kelee* (from Day, *Fishes of India*, modified).

Body strongly compressed, its depth a little greater than head length. Snout a little smaller than eye diameter, pre-orbital length (i.e. including eye) equal to post-orbital length. Lower jaw included when mouth firmly shut ; maxilla length equals pre-orbital length, extending to below middle or posterior part of eye ; exposed portion with longitudinal ridges ; two supra-maxillae. Pseudobranch shape as in Figure 6B ; a groove present below base of pseudobranch. Dorsal with low scaly sheath ; dorsal origin just nearer to snout tip than to caudal base ; pelvic origin below 3rd-5th branched dorsal rays, usually nearer to caudal base than to snout. Pectorals not reaching pelvic base ; in larger fishes, a groove, to receive upper edge of pectoral ; no axillary pectoral scale. Pelvics about three-fifths of pectorals, nearer to pectoral base than to anal origin ; axillary scale present, about three-quarters length of fin. Anal with low scaly sheath ; anal origin slightly nearer to caudal base than to pelvic base. Caudal fin just longer than head, lower lobe longer than upper.

No teeth. Cutaneous sensory canals of head branching over suborbitals, pre-operculum, operculum, and extending onto scales behind head. Adipose eyelid with vertical slit exposing three-quarters of pupil. Dorsal surface of head with thin cutaneous covering, numerous fronto-parietal striae exposed, as shown in Figure 1A.

Cleithral lobe prominent (Figure 3A). Gill filaments of outer hemibranch on first arch about half length of those of the inner hemibranch (Figure 3A). Gillrakers of second to fourth arches curled outwards, about 100 short serrae along inner margin of each raker (Figure 4B); gillrakers on lower part of first arch longer than corresponding gill filaments. Opercular bones as in Figure 5A.

Dorsal iv 13-14, pelvic i 7, anal iii 17-19. Pre-pelvic scutes 16 (Regan gives 16-18), post-pelvic scutes 12-13 (Regan 11-13), total 28-30. Scales in lateral series 42-45, 13-14 in transverse series (after Regan). Gillrakers fine and numerous, about 100-150 on lower part of first arch.

COLOUR IN ALCOHOL: Back and upper parts of head brown, flanks silvery. A dark humeral blotch followed (in some specimens) by seven or eight smaller black blotches. Tips of anterior dorsal rays dusky, caudal tips faintly dusky.

DISTRIBUTION: Natal, East African coast, Gulf of Aden, coasts of India, Burma and Siam. The record from Amoy (Wu 1929) was perhaps based on a juvenile of *H. reevesii*, as also a Cambodia record (Chevey and Le Poulain 1940).

SIZE: Up to 220 mm. (Regan).

TYPE MATERIAL: The type of *Hilsa kelee* is Russell's figure of Keelee. Although a poor drawing by modern standards, it is adequate to establish the identity of the species. I have found no reference to any specimens of *H. kelee* on which Russell might have based his drawing. The type of *Alosa brevis* Bleeker was apparently lost shortly after its description (Bleeker 1872). The holotype of *Clupea platygaster* Günther, a syntype of *Alausa kanagurta* Bleeker, and the syntypes of *Clupea durbanensis* were examined and are listed below.

Study Material.

- 1 fish, 130 mm., purchd. of Mr. Franks (1862.2.4.10).
- 1 fish, 132 mm., purchd. of Mr. Damon (1866.8.14.100).
- 1 fish, 98 mm., Bleeker Collection (1867.11.28.25).
- 5 fishes, 83-117 mm., Madras, coll. F. Day (1889.2.1.1979-83).
- 1 fish, 117 mm., Orissa, coll. F. Day (1889.2.1.1986).
- 1 fish, 89 mm., Kurrachee, coll. F. W. Townsend (1898.12.24.59).
- 1 fish, 48 mm., Sabaki mouth, Kenya (1955.1.18.1).
- 4 fishes, 129-133 mm., Aden, coll. Fraser-Brunner (1962.3.26.202-205).
- 5 fishes, 65-91 mm., Jibuti, coll. Fraser-Brunner (1962.3.26.206-210).
- 1 fish, 103 mm., *Alausa brachysoma* Bleeker HOLOTYPE of *Clupea platygaster* Günther), Padang, Sumatra, purchd. of Dr. Bleeker (1867.11.28.24).
- 1 fish, 132 mm., SYNTYPE of *Alausa kanagurta* Bleeker, no locality (1867.11.28.26).
- 1 fish, 90 mm., "*Harengula (Paralosa) zeylanica*" of Sale Catalogue (1879), Ceylon? (Rijksmuseum, Leiden, No. 7495) (unpublished Bleeker name).
- 2 fishes, 169 and 180 mm., SYNTYPES of *Clupea durbanensis* Regan, Durban (1905.6.8.19-20).
- 1 fish, 76 mm., Durban, Natal (1919.4.1.1).
- 2 fishes, 67 and 180 mm., Durban, Natal (1919.9.12.1-2).

1 fish, 116 mm., Durban, Natal (1915.7.6.2).

(Dry specimens)

1 fish, 102 mm., Pinang (*Alausa toli* from Cantor's collection) (1860.3.19.439).

1 fish, 130 mm., Zanzibar, Playfair Collection (1867.3.9.371).

Subgenus *Tenualosa*

As defined in the key, p. 127. Four species recognised here.

KEY TO THE SPECIES of *Tenualosa*

- I Caudal lobes as long as head ; pseudobranch rather attenuated and with groove below (Figure 6A).
- a Upper (exposed) border of suboperculum contained more than twice in depth of operculum ; scales 45-48 in lateral series ; coasts and rivers from Arabia to Burma ***H. (Tenualosa) ilisha***
- b Upper (exposed) border of suboperculum contained less than twice in depth of operculum ; scales 42-45 in lateral series ; coasts and rivers of China
H. (Tenualosa) reevesii
- II Caudal lobes longer than head ; pseudobranch not attenuated, without ventral groove (Figure 6B).
- a Maxilla short, not reaching eye centre ; suboperculum almost rectangular, its upper (exposed) border almost horizontal ; cleithral lobe small but present
H. (Tenualosa) macrura
- b Maxilla longer, reaching eye centre or beyond ; suboperculum with rounded posterior margin, upper (exposed) border more steeply inclined, as in Figure 5A ; cleithral lobe barely apparent, as in Figure 3B ***H. (Tenualosa) toli***

H. macrura, with very long caudal lobes and a short maxilla, is fairly distinctive, but *H. ilisha*, *H. toli* and *H. reevesii* are extremely alike, especially in juvenile stages. In examining stuffed specimens, where the pseudobranch character cannot be checked and where the caudal lobes are often damaged, it is difficult to distinguish between *H. toli* and *H. ilisha*. The difference between these two species in scale counts and in the lengths of the maxilla, head and caudal lobes might perhaps be ascribed to mere geographical variation. But the difference in pseudobranch shape, and the presence or absence of a groove below it, appear to be sufficiently consistent for the two species to be kept separate. *H. reevesii*, on the other hand, may yet prove to be only a subspecies of *H. ilisha* when more specimens are available.

Hilsa ilisha (Ham. Buch.)

Clupanodon ilisha Hamilton-Buchanan, 1822, *Fishes of the Ganges* : 243, 382, pl. 19, fig. 73 (type material from : Ganges estuaries, Patua, Goya Rarra, Calcutta, Dhasa).

Alausa ilisha : Cantor, 1850, *J. Asiatic Soc. Bengal*, **18** : 1282 ; Bleeker, 1852, *Verh. Bat. Gen.*, **24** : 33 ; Kner, 1865, *Reise Novarra, Fische* : 331.

Clupea ilisha : Day, 1878, *Fishes of India*, pt. 4 : 640, pl. 172, fig. 3 ; *Idem*, 1889, *Fauna Brit. India, Fishes*, **1** : 376, fig. 115 ; Lloyd, 1907, *Rec. Ind. Mus.*, **1** : 221 ; Tirant, 1929, *Serv. océanogr. Pêches Indo-Chine*, 6^e note : 118.

- Clupea (Alosa) ilisha* : Steindachner, 1896, *Ann. Hofmus. Wien.*, **11** : 228.
- Hilsa ilisha* : Regan, 1917, *Ann. Mag. nat. Hist.*, (8) **19** : 306 ; Fowler, 1934, *Proc. Acad. nat. Sci. Philad.*, **85** : 246 ; Shaw & Shebbeare, 1937, *J. Asiatic Soc. Bengal*, **3** : 13 ; Bertin, 1940, *Bull. Mus. Hist. nat. Paris*, (2) **12** : 281 ; Blegvad, 1944, *Danish Sci. Invest. Iran*, pt. 3 : 63, fig. 28 ; Misra, 1947, *Rec. Ind. Mus.*, **45** (4) : 389 ; Pillay, 1952, *Proc. Indo-Pac. Fish. Council.*, **3** (Section 2 s 2/8) ; Pillay, 1954, *J. Asiatic Soc. Bengal*, **20** (1) : 69 ; *Idem*, 1957, *Indian J. Fish.*, **4** (2) : 345 ; Quereshi, 1957, *Agric. Pakistan*, **8** (2) : 104, fig. 6a ; Khalaf, 1961, *Fishes of Iraq, Baghdad* : 17 ; Mahdi, 1962, *Fishes of Iraq, Baghdad* : 11 ; Pillay & Rosa, 1963, *FAO Fish. Biol. Synopsis* No. 25 : 1, figs. 1 (adult), 3 (embryos), 4-6 larvae and juveniles).
- Macrura ilisha* : Fowler, 1941, *Bull. U.S. nat. Mus.*, No. 100 : 633 ; *Idem*, 1956, *Fishes of Red Sea*, **1** : 69.
- Tenualosa ilisha* : Munro, 1955, *Mar. F-water Fishes Ceylon* : 25.
- Clupea palasah* Cuvier, 1829, *Règne animal*, ed. 2, **2** : 320 (on *Palasah* Russell, 1803, *Fishes of Coromandel*, **2** : 77, pl. 198 (type locality, Vizagapatam) ; Günther, 1868, *Cat. Fish. Brit. Mus.*, **7** : 445.
- Alausa palasah* : Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 432 (*part*, i.e. Ganges and Malabar specimens only) ; Jerdon, 1849, *Madras J. Lit. Soc.*, **15** : 345 ; Day, 1865, *Fishes of Malabar* : 235.
- Clupea (Alosa) palasah* : Steindachner, 1896, *Ann. Hofmus. Wien*, **11** : 229.

Note on synonymy.

The description of *Clupea ilisha* given by Hamilton-Buchanan (1822) must be presumed to refer to this species, even though the figure shows a fish with the short maxilla (not reaching posterior eye border) and a suggestion of the longitudinal ridges on the maxilla characteristic of *H. kelee*. However, the latter species can be excluded since Hamilton-Buchanan emphasises the presence of pectoral axillary scales, which are absent in *H. kelee* ; also, the dorsal view of the head shows no fronto-parietal striae. Hamilton-Buchanan distinguished his species from the *Palasah* of Russell (1803, p. 77, pl. 198) because of a very slight difference in fin-ray counts and because the *Palasah* apparently lacked pelvic axillary scales ; such pelvic axillary scales are, however, present in all species of *Hilsa*. Since Russell also describes a pectoral axillary scale, and since neither Russell nor Hamilton-Buchanan show the long caudal lobes characteristic of *H. toli* and *H. macrura*, it must be presumed that both were referring to the present species. Bleeker (1852) similarly made a distinction between *Palasah* and this species, mainly on pectoral length ; but the pectorals in *H. ilisha* vary in length (in my material), sometimes reaching the pelvic base and sometimes falling far short of this point.

As mentioned earlier, much of the material listed by Günther (1868, p. 446) under *Clupea ilisha* can be referred to *H. kelee*. There is, however, a specimen (skin) from Cantor's collection (225 mm., Ikan Truboh) which may be *H. toli* ; there are only 40 scales in lateral series (*H. ilisha* 45-48) but the (damaged) caudal lobes seem to be too short. Unfortunately the diagnostic pseudobranch character cannot be checked.

Three of the four stuffed specimens listed by Günther (p. 445) under *Clupea palasah* are *H. ilisha* ; one Gangetic specimen is missing.

Of the fishes mentioned by Valenciennes under *Alausa palasah*, two specimens from the Ganges and one from Malabar are *H. ilisha*, but a specimen from Bombay

and one from Pondicherry are *H. toli*.

DESCRIPTION. Based on 24 fishes, 99–325 mm. standard length from the coasts of India, and from the Persian Gulf and the River Tigris (see list of study material).

In percentages of standard length : body depth 31.0–39.5, head length 28.6–33.5 ; snout length 5.8–7.3, eye diameter 4.6–6.8, maxilla length 12.2–14.5 ; operculum, height 13.6–15.7, breadth 7.5–9.6 ; pectoral length 18.3–21.5, pelvic length 10.8–12.8, caudal length 25.7–33.2 ; pre-dorsal distance 47.0–52.0, pre-pelvic distance 51.0–55.0. In relation to standard length, eye diameter shows negative allometry, and there is an indication that pectoral and pelvic lengths may show positive allometry.

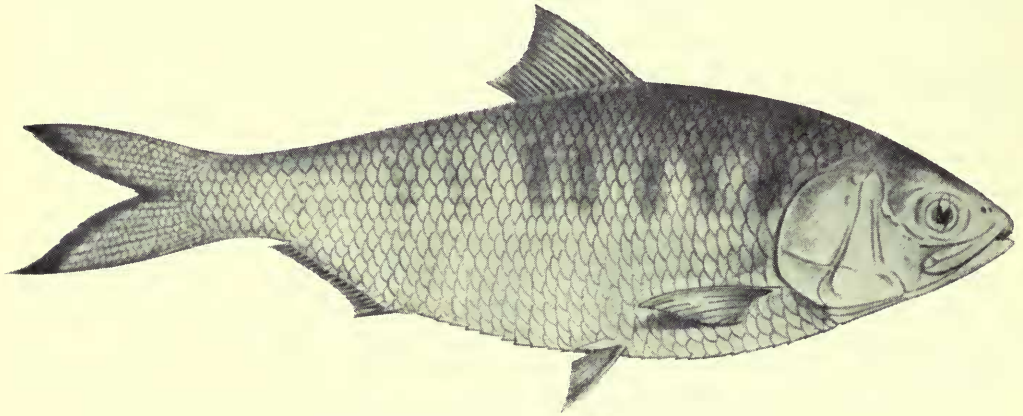


FIG. 9. *Hilsa ilisha* (from Day, *Fishes of India*, modified).

Body strongly compressed, its depth variable, a little greater than head length. Snout greater than eye diameter in fishes over about 100 mm., less than eye diameter below this ; pre-orbital length (including eye) two-thirds of post-orbital length. Lower jaw included when mouth firmly shut ; maxilla length just less than pre-orbital length, extending almost to posterior border of eye, exposed portion without longitudinal ridges but occasionally with faint longitudinal striae ; two supra-maxillae. Pseudobranch attenuated, as shown in Figure 6A ; a groove present below border of pseudobranch. Dorsal with low scaly sheath ; dorsal origin just nearer snout tip than base of caudal ; pelvic origin below 1st–4th branched dorsal rays, just nearer to caudal base than to snout. Pectorals variable, sometimes reaching pelvic base ; axillary scale present, half length of pectoral. Pelvic fins about three-fifths length of pectorals, nearer to pectoral base than to anal origin ; axillary scale present, about half length of fin. Anal with scaly sheath ; anal origin equidistant between pelvic base and caudal base ; anal longer than in *H. reevesii*, its base greater than distance snout tip to anterior margin of pre-operculum. Caudal fin equal to or just shorter than head length, lower lobe longer than upper.

No teeth. Cutaneous sensory canals of head branching over suborbitals, pre-

operculum, operculum, and extending onto scales behind head. Adipose eyelid with vertical slit exposing three-quarters of pupil.

Dorsal surface of head thickly covered by skin, no fronto-parietal striae, but lateral margins of frontals may show one or two longitudinal ridges through skin (see Figure 1B). Cleithral lobe not prominent, barely interrupting cleithral outline (Figure 3B). Gill filaments of outer hemibranch on first arch half to three-quarters length of those of inner hemibranch (Figure 3B). Gillrakers on all arches straight or slightly curved, not curled outwards, tips pointed, as long as corresponding gill filaments in adults (Figure 4A). Bones of opercular series resembling those of *H. kelee* (Figure 5A).

Dorsal iv-v 14-16, pelvic i 7, anal ii-iii 18-20, branchiostegal rays 5. Pre-pelvic scutes* (14) 15-19, post pelvic scutes (10) 11-15 (16), total (26) 27-32 (33) (612 fishes). Scales in lateral series (39-44) 45-49 (49) (443 fishes), in transverse series 17-20 ; exposed portion of scales with numerous longitudinal striae, edge of scale pectinated, especially in larger fishes ; minute scales covering caudal, except along posterior border. Gillrakers fine and numerous, 120 (young) to 200 on lower part of first arch (after Regan). Trunk vertebrae 12-13, caudal vertebrae without haemal spines (10) 11-12 (13), caudal vertebrae with haemal spines 20-22 (23), total vertebrae (44) 45-46 (114 fishes).

The regressions of various body measurements on standard length for Hooghly river and Chilka Lake specimens were calculated by Pillay (1957), who showed significant differences between samples from these two localities in five non-meristic characters. Pillay and Rosa (1963), summarising earlier studies, stated that " each major river system, the Chilka Lake and the Saurashtra Coast have their own stocks of *hilsa* and there is very little, if any, intermingling among them". The differences between these stocks involve meristic as well as non-meristic characters, and in addition, fishermen report differences in taste (dependent probably on fat content).

The skull of *H. ilisha* has been described and figured by Moona (1959), the pharyngeal pockets by Kapoor (1955), the swim-bladder by Srivastava (1955), blood characteristics by Pillay (1954, 1958), and the branchial skeleton by Khanna (1961).

COLOUR : " Silvery, shot with gold and purple ; no spots in the adult, but a row of them along the upper third of the body in the immature " (Pillay & Rosa) ; in alcohol, body brown, sometimes still silvery, upper surfaces darker, fins hyaline.

Bionomics, fishery, etc. :

H. ilisha has considerable economic importance in Indian waters (especially in the Bay of Bengal) and in Pakistan and Burma. Following a symposium in 1952, current information on the *Hilsa* fisheries was assembled (*J. Asiatic Soc.*, 20 (1) : 1-79 (1954)) by the Hilsa Sub-Committee of the Indo-Pacific Fisheries Council. The many papers dealing with the bionomics, life history and fishery of *H. ilisha* published since then have been usefully summarised by Pillay and Rosa (1963).

The esteem in which the ' hilsa ' is held in Bengal is reflected in the many references

*Scute, scale and vertebral counts are from Hooghly river and Chilka Lake specimens examined by Pillay (1957) ; rare counts placed in parenthesis. My material lies well within these ranges.

to its quality and flavour in Sanskrit and Bengali literature,* while Day (1878) and other writers testify to the popularity of the 'sable fish' amongst Europeans.

SIZE : Females attain a larger size than males (Pillay & Rosa, 1963). On the Godavari, Chacko and Ganapati (1949) recorded females of 356–600 mm., and males of 300–432 mm. On the same river, Pillay and Rao (in Pillay & Rosa, 1963) record the smallest mature male as 256 mm., and the smallest mature female 370 mm., but in the Hooghly such mature fishes were smaller (160–170 mm. and 190–200 mm. respectively—see Pillay, 1958).

DISTRIBUTION : Persian Gulf (Tigris, Euphrates, Lake Hammar), West Pakistan (Indus), west coast of India, Ceylon, Bay of Bengal, deltaic area of Burma, coastal waters of Cochin China (see Pillay and Rosa, 1963).

TYPE MATERIAL : The type of *Hilsa ilisha* is Hamilton-Buchanan's figure (Pl. 19, fig. 73). It was based on a juvenile, which might account for the rather short maxilla. But the anal branched ray count (19) distinguishes it from *H. toli*, as also does the short caudal. The absence of fronto-parietal striae, and the presence of a pectoral axillary scale rule out *H. kelee*. Paratypes of *Alausa palasah* are listed below.

Study material.

- 3 fishes, 115–131 mm., Tigris (1875.1.14.11–13).
- 2 fishes, 208–290 mm., Calcutta (1889.2.1.1962–3).
- 9 fishes, 30–115 mm., Orissa (1889.2.1.1964–9) + (3 unregistered).
- 7 fishes, 52–101 mm., Madras (1889.2.1.1970–5) + (1 unregistered).
- 1 fish, 212 mm., Canara (1889.2.1.1976).
- 3 fishes, 68–79 mm., Sind (1889.2.1.1977–8) + (1 unregistered).
- 1 fish, 323 mm., Bombay (1889.2.1.2022).
- 6 fishes, 97–146 mm., Sittang R. (1891.11.30.396–401).
- 2 fishes, 297–323 mm., Ganges, PARATYPES of *Alausa palasah* Valenciennes (M.N.H.N. Paris No. 3685–6)
- 1 fish, 195 mm., Malabar, coll. Dussumier (M.N.H.N. Paris 4976).
- 1 fish, 325 mm., Ormara, Meknam Coast (1899.5.8.11).
- 6 fishes, 99–127 mm., Basra (1920.3.3.178–82) + (1 unregistered).
- 25 fishes, 63–135 mm., Padma R., Bengal (1923.6.30.1–10) + (15 unregistered).
- 1 fish, 108 mm., Bengal (1934.10.17.11).
- (Dry specimens)
- 1 fish, 350 mm., R. Tigris (1875.1.14.14).
- 1 fish, 360 mm., R. Tigris (1875.1.14.15).
- †1 fish, 370 mm., India (1861.4.2.2).
- 1 fish, 410 mm., Madras (1883.11.26.81).
- †1 fish, 340 mm., Suttapore, Ganges (1848.2.1.66).
- †1 fish, 300 mm., Suttapore, Ganges (1848.2.1.65).

*For example, hilsa is described as *matsyaraja* (king of fishes), and elsewhere it is said, *Illisah jitapiyusah* (Hilsa surpasses nectar)—see Hora 1954.

†*Clupea palasah* of Günther (Catalogue, p. 445).

Hilsa reevesii (Richardson)

- Alosa reevesii* Richardson, 1846, *Ichthy. China Japan* : 305 (type locality, China seas).
Alausa reevesii : Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 437 ; Sauvage, 1881, *Bull. Soc. Philom. Paris* (ser. 7) **5** : 107.
Clupea reevesii : Günther, 1868, *Cat. Fish. Brit. Mus.*, **7** : 446 ; Peters, 1880, *Monatsh. Akad. Wiss. Berlin* : 926 ; Günther, 1889, *Ann. Mag. nat. Hist.* (ser. 6) **4** : (219) 229 ; Elera, 1895, *Cat. Fauna Filip.*, **1** : 583 ; Rutter, 1897, *Proc. Acad. nat. Sci. Philad.* : 64.
Hilsa reevesii : Regan, 1917, *Ann. Mag. nat. Hist.*, (ser. 8) **19** : 306 ; Chu, 1931, *Biol. Bull. St. John's Univ.*, No. 1 : 13 ; Fowler, 1934, *Proc. Acad. nat. Sci. Philad.*, **85** : 246 ; Kimura, 1935, *J. Shanghai Sci. Inst.*, (sect. 3) **3** : 104 ; Mori, 1952, *Mem. Hyogo Univ. Ag.*, **1** (3) : 32.
Macrura reevesii : Fowler, 1941, *Bull. U.S. nat. Mus.*, No. 100 : 630.
Alausa palasah : (non Cuvier) Richardson, 1846, *Ichthy. China Japan* : 306 ; Cantor, 1849, *J. Asiatic Soc. Bengal*, **18** : 282 (based on Richardson's specimen).
? *Harengula kanagurta* : Wu, 1929, *Contr. Biol. Lab. Sci. Soc. China*, **5** (4) : 17, fig. 13.
? *Clupea (Alosa) thibaudeani* : Durand, 1940, *Notes Inst. océanogr. Indochine*, **36** : 6, fig. 1 ; Chevey & Le Poulain, 1940, *Trav. Inst. océanogr. Indochine*, 5^e mem. : 19.
? *Clupea (Alosa) kanagurta* : Chevey & Le Poulain, 1940, *Trav. Inst. océanogr. Indochine*, 5^e mem. : 19.

Note on synonymy.

Fowler (1941, p. 630) included *Clupea palasah* Günther in this synonymy, but as noted earlier, three of Günther's four specimens are *H. ilisha* and the fourth is missing.

Durand (1940) compared his *Clupea (Alosa) thibaudeani* with *H. kanagurta*, stating that his fishes had a broader operculum and more gillrakers (operculum breadth 1.5 in height, gillrakers 290). But Durand's figure shows a well-defined pectoral axillary scale, an upper suboperculum border rising very steeply and there is enough detail on the dorsal part of the head to suggest that fronto-parietal striae were absent. It seems likely that Durand's specimens belong to *Tenuualosa*, and the high gillraker count, low scale count (40-42) and low dorsal ray count (17) point to *H. reevesii* ; the broad operculum seems to confirm this. A series of black spots are shown on the flanks, but his specimens were 122-240 mm. and were probably juveniles.

The two references to *kanagurta* in the synonymy (from Amoy and Cambodia) are tentatively placed here, mainly on geographical grounds.

DESCRIPTION. Based on five fishes 150-500 mm. standard length from Hong Kong and China (see list of Study Material). Measurements as in *H. ilisha*.

In percentages of standard length : body depth 28.8-33.9, head length 27.4-31.7 ; snout length 6.8-7.5, eye diameter 3.6-6.5, maxilla length 11.2-13.3 ; operculum, height 12.2-15.0, breadth 8.2-9.5 ; pectoral length 18.0-18.8, pelvic length 9.6-11.5, caudal length 28.0-31.2 ; pre-dorsal distance 49.6-50.7, pre-pelvic distance 50.0-51.7. In relation to standard length, eye diameter shows strong negative allometry ; negative allometry may occur also in body depth and snout length in fishes up to 150 mm. in length.

Body strongly compressed, its depth a little greater than head length. Snout greater than eye diameter in fishes over about 150 mm. ; less than eye below this ; pre-orbital length (including eye) about two-thirds of post-orbital length. Lower

jaw included when mouth firmly shut ; maxilla length just equal to pre-orbital length, extending just to posterior border of eye, exposed portion without longitudinal ridges but with many fine longitudinal striae in large fishes ; two supra-maxillae. Pseudobranch attenuated, as in Figure 6A ; a groove present below lower border of pseudobranch, more pronounced in larger fishes. Dorsal with low scaly sheath ; dorsal origin about equidistant between snout tip and base of caudal ; pelvic origin below anterior unbranched dorsal rays, equidistant between snout tip and caudal base. Pectorals not reaching pelvic base ; axillary scale present, two-fifths length of pectoral. Pelvic fins half length of pectorals, nearer to pectoral base than to anal origin ; axillary scale present, just less than half length of fin. Anal with scaly sheath ; anal origin equidistant between pelvic tips and caudal base ; anal base shorter than in *H. ilisha*, less than distance from snout tip to anterior margin of pre-operculum. Caudal fin a little longer than head length, lower lobe longer than upper.

No teeth. Cutaneous sensory canals of head branching over sub-orbitals, pre-operculum, operculum, and extending onto scales behind head. Adipose eyelid with vertical slit exposing whole pupil.

Dorsal surface of head thickly covered by skin, no fronto-parietal striae, but lateral margins of frontals may show one or two longitudinal ridges through skin (see Figure 1B). Cleithral lobe not prominent, scarcely breaking cleithral outline (Figure 3B). Gill filaments of outer hemibranch on first arch half to three-quarters length of those of inner hemibranch (Figure 3B). Gillrakers on all arches straight or slightly curved, not curled outwards, tips pointed, as long as or slightly shorter than corresponding gill filaments. Bones of opercular series resembling those of *H. ilisha* but operculum broader, suboperculum longer, and junction between two rising more steeply ; upper (exposed) border of suboperculum less than twice in height of operculum.

Dorsal iv 13-15, pelvic i 7, anal iii 15-17. Branchiostegal rays 5. Pre-pelvic scutes 17*, post-pelvic 14-15, total 31-32. Scales in lateral series 40 (Fowler) 42-45, in transverse series 16-17 (Regan) ; exposed portion of scales with numerous longitudinal striae, edge of scale pectinated in larger fishes ; minute scales on caudal, except along posterior border. Gillrakers fine and numerous, 150 (young) to 250 on lower part of first arch (after Regan).

COLOUR : In alcohol, upper surfaces brown, flanks silvery or golden, no spots on upper part of flank in larger fishes, but a faint series in a specimen of 65 mm. "*Extrémité des pectorals largement rembrunie (en eau formolée)*" (Chabanaud 1936).

SIZE : Up to 575 mm. standard length.

DISTRIBUTION : China Seas, Shanghai, Kiukiang, Hong Kong ; Philippines (Elera's records) ; Korea (Fusan) rare (Mori 1952) ; Cambodia (Durand 1940).

TYPE : A mounted skin, as listed under Study Material.

*Regan (1917) records 18 + 13-14 for the same material, evidently counting as a pre-pelvic scute the small scute between the bases of the pelvics.

Relationship to H. ilisha.

H. reevesii and *H. ilisha* are evidently closely related, the former replacing the latter along the coasts of China. On the basis of my (admittedly meagre) material I am keeping the two separate since further small differences besides that of operculum shape have emerged from analysis of available data.

In *H. reevesii* the pelvic fins are set slightly nearer the snout and, possibly as a result, the anal origin is equidistant between the pelvic *tips* and the caudal base, (pelvic *base* and caudal base in *H. ilisha*). In addition, the anal has slightly fewer branched rays in *H. reevesii* (15-17 ; cf 18-20) and the base of the anal is noticeably shorter. Thus, in *H. ilisha*, the anal base is almost as long or longer than the pectorals and equal or greater than the distance snout tip to anterior pre-operculum margin ; in *H. reevesii*, the anal base is about two-thirds pectoral length and, measured from snout tip, reaches the posterior border of the eye (juveniles) or a little beyond (adults).

I have included Elera's Philippine records, although these do not appear to have been validated since. If the records of *H. ilisha* from Cochin China are correct, then the Indo-Malayan Archipelago is not the boundary between these two species.

Study Material.

1 fish, 445 mm., China (1934.3.5.1).

1 fish, 365 mm., China (1884.2.26.75).

1 fish, 500 mm., Shanghai (1895.5.31.24)

1 fish, 65 mm., Amoy, China (1928.6.22.1).

1 fish, 234 mm., Hong Kong (1939.3.23.4).

1 fish, 150 mm., China (coll. Reeves) (1963.8.20.1).

2 fishes, 570-575 mm., Kiu Kiang (1888.3.23.44-45).

(Dry specimens)

1 fish, 295 mm., HOLOTYPE of *Clupea reevesii*, China (coll. Reeves) (1963.8.20.2).

1 fish, 140 mm., China (coll. Reeves) (1963.8.20.3).

Hilsa macrura (Bleeker)

Alosa macrurus Bleeker, 1852, *Verh. Bat. Gen.*, **24** : 31 (on *macrura* Kuhl & van Hasselt 1823) (type locality, Batavia, Java).

Alosa macrurus : Bleeker, 1861, *Versl. Meded. Akad. Wet. Amsterdam*, **12** : 64 ; *Idem*, 1868, *op. cit.*, (ser. 2) **2** : 294 ; *Idem*, 1872, *Atlas Ichth. Ind. Néerland*, **6** : 113, pl. 264, fig. 4.

Clupea macrura (Kuhl & van Hasselt) : Bleeker, 1852, *Verh. Bat. Gen.*, **24** : 31 (name in synonymy) ; Günther, 1868, *Cat. Fish. Brit. Mus.*, **7** : 448 ; Vinciguerra, 1926, *Ann. Mus. Civ. Stor. nat. Genoa* (ser. 3) **10** : 619 ; Tirant, 1929, *Serv. océanogr. Pêches Indo-Chine*, 6^e note : 119, 174 ; Hardenberg, 1931, *Treubia*, **13** (1) : 111.

Clupea (Alosa) macrura : Weber & de Beaufort, 1913, *Fish. Indo-Aust. Arch.*, **2** : 65 ; Chevey, 1932, *Inst. océanogr. Indo-Chine*, 19^e note : 9.

Hilsa macrura : Regan, 1917, *Ann. Mag. nat. Hist.* (ser. 8) **19** : 307 ; Fowler, 1934, *Proc. Acad. nat. Sci. Philad.*, **85** : 246 ; *Idem*, 1938, *List Fish. Malaya* : 27.

Macrura macrura : Fowler, 1941, *Bull. U.S. nat. Mus.*, No. 100 : 632.

Note on synonymy.

As noted below (p. 145), Bleeker's original description of *Alausa macrurus* was based entirely on a figure prepared by Kuhl and van Hasselt, stated by Bleeker to be 310 mm. (Kuhl and van Hasselt are known to have made their drawings life-size wherever possible). A Kuhl and van Hasselt specimen of 420 mm. in the Leiden Museum is thus too large to have been the fish from which the drawing was made. Dr. Boesman informs me (*in litt.*) that this fish is labelled "*Clupea macrura*", but that there is also a second (old) label "*Clup. palasah* Cuv.". He considers the specimen to be *Hilsa toli* and makes the suggestion that from this specimen a second drawing of *Clupea macrura* may have been made by Kuhl and van Hasselt, and that it was this second drawing that Valenciennes saw and identified (correctly) as *tolii*. Whatever the truth in this, it seems certain that no Kuhl and van Hasselt specimen of *Hilsa macrura* exists, and that Bleeker should be accorded authorship of this name.

The type of *Alausa macrurus* Bleeker 1852 is not the Kuhl and van Hasselt drawing on which Bleeker based his description, because this figure was never published (a further reason for considering Bleeker the true author of this name). It is therefore necessary to select a neotype from amongst Bleeker's material.

Bleeker (1853, p. 502) records his first specimen from Batavia, a fish of 342 mm. total length. This fish can be identified with a specimen in the Bleeker collection at the Leiden museum (the larger of two, RMNH 7112) which is 245 mm. standard length and 337+ mm. total length (caudal tips damaged). This specimen is here designated neotype. Dr. Boesman has examined this fish and confirmed its identity for me. The specimen from Bleeker's collection supposed by Günther (1868, p. 448) to be the type of *Clupea macrura* appears to be lost. Bertin (1940) listed a supposed cotype of *Alausa macrurus* Bleeker in the Paris Museum. This fish is *Hilsa macrura* but probably derives from a later collection by Bleeker than that from which the neotype has been selected.

DESCRIPTION. Based on 2 fishes, 141 and 151 mm. standard length from Sarawak; and one fish 181 mm., a Bleeker specimen (see list of Study Material).

In percentages of standard length: body depth (33.7) 37.7-38.0, head length 24.0-25.4; snout length 4.9-5.4, eye diameter 5.5-5.8, maxilla length 8.1-8.8; operculum, height 11.4-12.9, breadth 5.8-6.4; pectoral length 19.9, pelvic length 9.9-11.5, caudal length 46.3-46.5; pre-dorsal distance 46.5-48.8, pre-pelvic distance 49.7-51.3. Regan (1917) implies that caudal lobes show positive allometry in relation to head length.

Body strongly compressed, head length about two-thirds of body depth. Snout less than eye diameter; pre-orbital length (including eye) almost equal to post-orbital length. Lower jaw included when mouth firmly shut; maxilla length three-quarters of pre-orbital length, reaching to eye centre; exposed portion smooth, without longitudinal ridges or striae; two supra-maxillae. Dorsal with low scaly sheath; dorsal origin a little nearer to snout tip than to base of caudal; pelvic origin below 3rd-4th branched dorsal rays, equidistant between snout tip and caudal base. Pectorals not reaching pelvic base; axillary scale present, almost three-quarter pectoral length. Pelvic fins about half length of pectorals, a little nearer

to pectoral base than to anal origin ; axillary scale present, three-quarters length of fin. Anal with low scaly sheath ; anal origin equidistant between pelvic base and caudal base. Caudal fin almost twice head length, lower lobe a little longer than upper.

No teeth. Cutaneous sensory canals of head branching over suborbitals, preoperculum, operculum, and extending onto scales behind head. Adipose eyelid with vertical slit exposing whole pupil.

Dorsal surface of head covered with thick skin, no fronto-parietal striae, but lateral margins of frontals may show one or two longitudinal ridges visible through skin. Cleithral lobe intermediate between that of *H. kelee* and *H. ilisha*, to some extent interrupting cleithral outline. Gill filaments of outer hemibranch of first arch three-quarter length of those of inner hemibranch. Gillrakers on all arches straight or slightly curved, with a small distal knob (Figure 4c), half length of corresponding gill filaments. Operculum bones as in *H. kelee* but suboperculum more rectangular, and the line of its (exposed) border with the operculum nearer the horizontal (if projected, cutting the dorsal profile far behind the dorsal fin).

Dorsal iv-v 15, pelvic i 7, anal iii 17, branchiostegal rays 5. Pre-pelvic scutes 17 (Regan 16-18, but see footnote p. 140), post-pelvic 14, total 31. Scales in lateral series 45, in transverse series 14-15 (Regan) ; minute longitudinal striae along posterior border of scale ; minute scales covering caudal lobes except along posterior border. Gillrakers fine and numerous, 60-80 on lower part of anterior arch (Regan).

COLOUR : In alcohol, dorsal surfaces brown, flanks silvery or golden, a faint dark humeral spot visible ; fins colourless except for faint dark edge to caudal.

SIZE : 350 mm. (Regan).

DISTRIBUTION : Java, Sumatra, Bankalis, Borneo, Singapore (Weber and de Beaufort, 1913). According to the latter authors " it forms the object of a very important fishery at the mouth of some rivers in Borneo, Malacca and Sumatra ".

TYPE : Neotype, a fish 245 mm. standard length (total length *ca* 337 mm., but caudal tips damaged), Reg. No. RMNH 7112, in the Bleeker collection at the Rijksmuseum van Natuurlijke Historie, Leiden, identified as Bleeker's first specimen from Batavia (see above, p. 142).

Study Material.

1 fish, 151 mm., Sarawak (1868.6.9.2).

1 fish, 141 mm., Sarawak (1895.2.28.72).

1 fish, 181 mm., East Indies, coll. Bleeker (M.N.H.N. Paris No. 2039).

Regan (1917) records a specimen of 350 mm. but I have been unable to find this fish.

Hilsa toli (Valenciennes)

Alausa toli Valenciennes,* 1847, *Hist. Nat. Poiss.*, 20 : 435 (type locality, Coromandel, Pondicherry) ; Cantor, 1849, *J. Asiatic Soc. Bengal*, 18 : 1281.

*Following Bailey (1951) I have throughout cited Valenciennes as sole author of volume 20 of the *Histoire Naturelle des Poissons*, 1847.

- Alosa toli* : Bleeker, 1872, *Atlas Ichth. Ind. Néerland.*, **6** : 113, pl. 265, fig. 4.
- Clupea toli* : Günther, 1868, *Cat. Fish. Brit. Mus.*, **7** : 447 ; Day, 1878, *Fishes of India*, pt. 4 : 641 ; *Idem*, 1889, *Fauna of Brit. India*, **1** : 377 ; Duncker, 1904, *Mitt. Naturhist. Mus. Hamburg*, **21** : 186 ; Pillay, 1929, *J. Bombay nat. Hist. Soc.*, **33** : 355 ; Tirant, 1929, *Serv. océanogr. Pêches Indo-Chine*, 6^e note : 119 ; Hardenberg, 1931, *Treubia*, **13** (1) : 110 ; *Idem*, *op. cit.*, **15** (3) : 231.
- Clupea (Alosa) toli* : Martens, 1876, *Preuss. Exped. Ost-Asien*, **1** : 405.
- Clupea (Alosa) toli* : Weber & de Beaufort, 1913, *Fishes Indo-Aust. Arch.*, **2** : 64 ; Chevy, 1932 (Aug. 25th), *Inst. océanogr. Indo-Chine*, 19^e note : 9.
- Sardinella toli* : Jordan & Evermann, 1902, *Proc. U.S. nat. Mus.*, **25** : 166 ; Jordan & Richardson, 1909, *Mem. Carnegie Mus.*, **4** : 166.
- Hilsa toli* : Regan, 1917, *Ann. Mag. nat. Hist.*, (8) **19** : 306 ; Hora, 1923, *J. nat. Hist. Soc. Siam*, **6** : 174 ; Chu, 1931, *Biol. Bull. St. John's Univ.*, No. 1 : 14 ; Herre & Myers, 1937, *Raffles Mus. Bull.*, No. 13 : 12 ; Smith, 1945, *Bull. U.S. nat. Mus.*, No. 188 : 44 ; Misra, 1947, *Rec. Ind. Mus.*, **45** (4) : 390 ; Quereshi, 1957, *Agric. Pakistan*, **8** (2) : 104, fig. 7.
- Alosa palasah* : Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 432 (*part*, i.e. Bombay and Pondicherry specimens).
- ?*Clupea macroura* (Kuhl & van Hasselt) Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 437 (name only ; misspelt).
- Alosa argyrochloris* Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 440 (type locality : Ile de France) (the single Dussumier specimen, not the two Quoy & Gaimard specimens—see below).
- Alosa clenolepis* Bleeker, 1852, *Natuurk. Tijdschr. Ned. Ind.*, **3** : 74 (type locality, Batavia, Muntok, Singapore).
- Clupea chapra* : (*non* Ham.-Buch.), Günther, 1868, *Cat. Fish. Brit. Mus.*, **7** : 447 ; Beavan 1877, *F-water Fish. India* : 118.
- Alosa ilisha* : (*non* Ham.-Buch.), Bleeker, 1874, *Ned. Tijdschr. Dierk.*, **4** : 148.
- ?*Clupea ilisha* : Günther (*part*), 1868, *Cat. Fish. Brit. Mus.*, **7** : 445.
- Hilsa sinensis* : Fowler, 1930, *Proc. Acad. nat. sci. Philad.* (1929) : 592, 598 ; *Idem*, 1938, *List Fish. Malaya* : 28.
- Tenualosa sinensis* : Munro, 1955, *Mar. F-water Fishes Ceylon* : 24.
- Macrura sinensis* : Fowler, 1941, *Bull. U.S. nat. Mus.*, No. 100 : 631 ; Chu & Tsai, 1958, *Quart. J. Taiwan Mus.*, **2** (1-2) : 104.

Note on synonymy.

Fowler (1930) identified this species with *Clupea sinensis* Bloch 1795 and later (Fowler 1941) included it in the synonymy of *Clupea sinensis* Linnaeus. But Linnaeus' description of *C. sinensis*, which appears for the first time in the tenth edition of the *Systema Naturae*, is too vague for a positive identification to be made (Valenciennes (1847) comments on this and concludes that *Clupea sinensis* Linnaeus, together with *Clupanodon sinensis* Lacepède "doit être rayé de nos catalogues ichthyologiques"). Of possible Chinese clupeids with moderate anal fins (i.e. about 16 rays) the gizzard shads can be eliminated since a filamentous last dorsal ray is not mentioned ; the dussumieriids *Dussumieria* and *Etrumeus* have too many branchiostegal rays (6 in *C. sinensis*) and *Spratelloides* has too few anal rays (16 in *C. sinensis*) ; *Sardinops* and *Clupea* are possible, but Linnaeus states that *C. sinensis* is similar to *Clupea harengus* "sed latior".

Daubenton (1787, p. 202) translates this as "sa largeur est plus considérable". It is the possibility that depth rather than overall size was meant which prevents exclusion of either *Sardinella* or *Herklotsichthys* from consideration.

Herklotsichthys (*Harengula* auct.) and *Sardinella* are possible since both have the appearance of truncated posterior branchiostegal rays, a character stressed in Linnaeus' description. In both *Herklotsichthys* and *Sardinella*, certain species or individuals either lack, or have feebly developed teeth ("os edentulum" in *C. sinensis*). On the other hand, neither *Herklotsichthys* nor *Sardinella* attain the size of *Hilsa*. Within *Hilsa* itself, *H. reevesii* is also a possibility. But since *Clupea sinensis* does not appear amongst the Linnaean type specimens at Uppsala University listed by Lönnberg (1896) and in view of the inadequacy of the original description I have here preferred to use Valenciennes' name *toli*.

C. sinensis L. of Bloch (1795) does not help to identify Linnaeus' fish. Bloch's figure shows a fish with a black mark at the base of the anterior dorsal rays, which is characteristic of some species of *Sardinella*. There is also a black border to the dorsal and the caudal, such as is found for example in *S. melanura* or *S. sindensis*. Valenciennes (*loc. cit.*) doubted Bloch's identification, believed Bloch's fish to have been different from Linnaeus', and called it *Clupeonia blochii* [placed by Day (1878) and Fowler (1941) in the synonymy of *H. kanagurta* (i.e. *H. kelee*)]. Day (*loc. cit.*), however, quotes Prof. Peters (*in. litt.*), who had examined a dried specimen and believed it to be the model for Bloch's figure, stating "I am of (the) opinion *C. sinensis* Bloch is *C. toli*, Cuv. and Val.". Peters also examined this specimen for Günther, who considered it identical to Hamilton-Buchanan's *Clupanodon ilisha* (Günther, 1868, p. 446). Unfortunately, most of Günther's 'ilisha' material is clearly *H. kanagurta* (see p. 130). I do not know whether this specimen is still extant, but the shortness of the maxilla and indeed of the whole head in Bloch's figure, as well as the distinctive black marks on the fins, are much more in accord with *Herklotsichthys* or *Sardinella* than with *Hilsa*. It can be noted, however, that Valenciennes (*loc. cit.* p. 436) describes black dorsal and anal borders in his *Alausa toli* (based on Dussumier's notes). The operculum is too narrow for *H. reevesii* and the caudal is too short for *H. toli*.

The *Clupea sinensis* (or Hareng de la Chine) of Bonnaterre (1788), Daubenton (1788), Ray (1788), Gmelin (1789), and Walbaum (1792) were based on Linnaeus' description; those of Martens (1876) and Schneider (1801) were based on Bloch.

A further problem concerning this synonymy is the identity of Kuhl and van Hasselt's *macrura*, a drawing of which both Valenciennes and Bleeker saw. Valenciennes (1847, p. 437) believed this fish to be his *Alausa toli*. However, Bleeker (1852, p. 32) maintained Kuhl and van Hasselt's name, showing that Valenciennes' *toli* had a longer head. In the Atlas, Bleeker (1872*) definitely separated the two species (on head length, jaw length and scales). Fowler (1941) tentatively placed *Clupea macroura* (K. v.H.) of Valenciennes in his synonymy for *H. toli*, while still accepting Bleeker's *macrura* as distinct. I have followed the same course, for reasons given in more detail under *H. macrura* (p. 142).

The single Dussumier specimen of *Alausa argyrochloris* Valenciennes is *Hilsa toli*, but the two Quoy and Gaimard specimens from Mauritius are *Sardinella*, probably *S. dayi* Regan. Bertin (1940) was therefore wrong to assume the latter to be para-

*I have here accepted the Atlas dating as reconstructed by Mees (1962).

topotypes of *H. toli*. Valenciennes' Bombay and Pondicherry specimens of *Alausa palasah* are also *H. toli*.

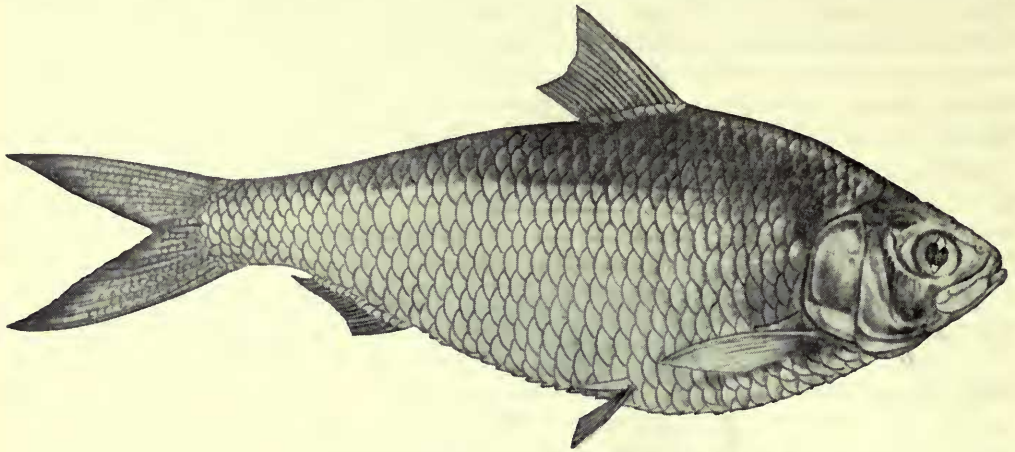


FIG. 10. *Hilsa toli* (from Day, *Fishes of India*, modified).

DESCRIPTION. Based on 11 fishes, 83–396 mm. standard length from the coasts of India and the Indo-Malayan Archipelago (including one of Bleeker's two specimens of *Alausa ctenolepis*, 420 mm. total length—see list of Study Material).

In percentages of standard length : body depth 32.6–39.0, head length 24.8–28.0 ; snout length 5.3–6.5, eye diameter 4.3–7.3, maxilla length 11.2–12.5 ; operculum, height 12.2–14.3, breadth 6.2–7.3 (8.6) ; pectoral length (16.2) 19.2–21.2, pelvic length (9.3) 10.3–13.1, caudal length 33.3–37.6 ; pre-dorsal distance 44.0–49.8, pre-pelvic distance 49.2–54.5. In relation to standard length, eye diameter shows strong negative allometry, and both pectoral and pelvic fins show positive allometry. In these specimens, smaller fishes have slightly deeper bodies.

Body strongly compressed, its depth greater than head length. Snout greater than eye diameter in fishes over about 120 mm., less than eye diameter in juveniles ; pre-orbital length (i.e. including eye) four-fifths of post-orbital length (equal in fishes of 100 mm. or less). Lower jaw included when mouth firmly shut ; maxilla length equal or (in large fishes) greater than pre-orbital length, extending beyond posterior eye border ; exposed portion without longitudinal ridges but occasionally with one or two faint longitudinal striae ; two supra-maxillae. Dorsal with low scaly sheath ; dorsal origin just nearer to snout tip than to caudal base ; pelvic origin below 4th–7th branched dorsal rays, equidistant or just nearer to caudal base than to snout. Pectorals not reaching pelvic base ; axillary scale present, half length of pectoral. Pelvic fins about half length of pectorals, just nearer to pectoral base than to anal origin ; axillary scale present, about two-thirds length of fin. Anal with low scaly sheath ; anal origin just nearer to caudal base than to pelvic base. Caudal fin a little longer than head length, lower lobe longer than upper.

No teeth. Cutaneous sensory canals of head branching over sub-orbitals, pre-operculum, operculum, and extending onto scales behind head. Adipose eyelid with vertical slit exposing all or three-quarters of pupil.

Dorsal surface of head thickly covered by skin, no fronto-parietal striae, but lateral margins of frontals may show one or two longitudinal ridges visible through skin. Cleithral lobe not prominent, barely interrupting cleithral outline. Gill filaments of outer hemibranch on first arch half to three-quarters length of those of inner hemibranch. Gillrakers on all arches straight or slightly curved, not curled outwards, tips pointed, as long as corresponding gill filaments in adults. Bones of opercular series as in *H. kelee*.

Dorsal iv-v 14-15, pelvic i 7, anal iii 15-17, branchiostegal rays 5. Pre-pelvic scutes 17 (Regan, 17-18), post-pelvic scutes 12-13 (Regan, 11-13), total 29-30. Scales in lateral series about 40, 14-15 in transverse series; exposed portion of scales with numerous longitudinal striae, edge of scale pectinate, especially in larger fishes; minute scales covering caudal, except along posterior border. Gillrakers fine and numerous, 70-95 on lower part of first arch (after Regan).

The swim-bladder of *H. toli* has been described by Nayak and Bal (1955), and the food and feeding habits by Chacko (1949).

COLOUR: "Silvery, shot with yellow and purple, a dark shoulder spot in young" (Day, 1878). In preserved material (alcohol), the back is brown, the flanks silver or golden, and the shoulder spot is very faint in the smaller specimens. In two small fishes (83 and 108 mm.) the caudal lobes are edged in brown; in the remainder, the fins are hyaline.

SIZE: 460 mm.

DISTRIBUTION: India, Malay Peninsula, Singapore, Pinang, East Indies, Siam, Formosa, China (Fowler, 1941).

TYPE MATERIAL: Bertin (1940) listed for this species only the holotype and paratypes of *Alausa argyrochloris* Valenciennes (discussed above). Dr. Blanc informs me that there are in fact two (dry) Valenciennes specimens in the Paris Museum (460 mm. *ex* Pondicherry, coll. Leschenault, No. 3939; and 440 mm. *ex* Bombay, coll. Roux, No. 3940), and has kindly examined them for me. Head lengths (24.3 and 25.0 per cent. of standard length respectively) confirm that the specimens are *H. toli* and not *H. ilisha*. Unfortunately, the caudals are both damaged (21.6 and 25.0 per cent. of S.L.) and the scale counts (39 and 39) are likely to be a little low. Since the locality and collector of the first fish (No. 3939) are those first mentioned by Valenciennes, this specimen is here designated lectotype.

Study Material.

*2 fishes, 83-108 mm., (Waterhouse collection—no locality) (1858.8.15.68-9).

1 fish, 121 mm., HOLOTYPE of *Alausa argyrochloris* (M.N.H.N.Paris No. 2738).

1 fish, 312 mm., HOLOTYPE of *Alausa ctenolepis* Bleeker, no locality (1867.11.28.23).

†1 fish, 216 mm., Pondicherry, coll. Bélanger (M.N.H.M.Paris No. 3687).

2 fishes, 122-124 mm., Orissa (1889.2.1.1984-5).

2 fishes, 276-396 mm., Bombay (1889.2.1.2018-19).

2 fishes, 110-163 mm., Bombay (1889.2.1.2020-21).

*Günther's *Clupea chapra* (Catalogue, p. 447).

- † 1 fish, 314 mm., Bombay, coll. Dussumier (M.N.H.N. Paris No. 3684).
 (Dry specimens)
 ? 1 skin, 225 mm., Ikan Truboh (Cantor collection) (1860.3.19.438).

Gudusia Fowler

Gudusia Fowler, 1911, *Proc. Acad. nat. Sci. Philad.*, **63** : 207 (type, *Clupanodon chapra* Hamilton-Buchanan).

Indo-Pacific alosinid fishes with very small scales, 80–100 in lateral series, 27–35 in transverse series. Scales adherent. Sub-operculum subrectangular or crescentic, its junction with the operculum, if produced, cutting the dorsal outline near or in front of the dorsal origin (Figure 5B).

Branchiostegal rays 6. Gillrakers numerous, 200 or more on lower part of first arch. Dorsal rays 14–16, pelvic 8, anal 20–24. Ventral scutes, 18–20 pre-pelvic and 8–10 post-pelvic.

Two species recognised here, from the rivers of India and Burma.

- 1 Depth less than 40 per cent. of S.L.; head more than 28 per cent.; anal iii 19–22

G. chapra

- 2 Depth more than 40 per cent. of S.L.; head less than 28 per cent.; anal iii 22–26

G. variegata

Gudusia chapra (Ham. Buch.)

Clupanodon chapra Hamilton-Buchanan, 1822, *Fishes of the Ganges* : 248, 383, (type locality, Upper Ganges).

Alosa chapra : Gray, 1832–34, *Illustr. Indian Zool. Hardwicke*, **2** : pl. 92, fig. 2.

Alausa chapra : Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 440.

Clupea chapra : Day, 1869, *Proc. zool. Soc. London* : 385 ; *Idem*, 1878, *Fishes of India*, pt. 4 : 639, pl. 161, fig. 1 ; *Idem*, 1889, *Fauna British India, Fishes*, **1** : 375.

Gudusia chapra : Fowler, 1911, *Proc. Acad. nat. Sci. Philad.*, **63** : 207 ; Regan, 1917, *Ann. Mag. nat. Hist.*, (8) **19** : 307 ; Fowler, 1938, *List. Fish. Malaya* : 26 ; *Idem*, 1941, *Bull. U.S. nat. Mus.*, No. 100 : 634.

Gadusia chapra : Chaturvedi, 1959, *Indo-Pac. Fish. Council. Occ. Paper* 60/2 : 2 (misspelling).

Clupea indica Gray, 1832–34, *Illustr. Indian Zool. Hardwicke*, **2** : pl. 19, figs. 1–2x ; Günther, 1868, *Cat. Fish. Brit. Mus.*, **7** : 444 ; Beavan, 1877, *F-water Fish. India* : 118.

?*Clupea champil* Gray, 1832–34, *Illustr. Indian Zool. Hardwicke*, **2** : pl. 91, figs. 5–6.

?*Pellona champil* : Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 324 (on Gray).

Alausa microlepis Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 439 ; Bleeker, 1853, *Verh. Bat. Gen.*, **25** : 146.

Clupea suhia Chaudhuri, 1912, *Rec. Ind. Mus.*, **7** : 436, pl. 38, fig. 1.

Note on synonymy.

Günther's description of *Clupea chapra* seems to refer to a species of *Hilsa* (scales 42, 13 post-pelvic scutes, anal 19) ; the two specimens listed by Günther are *H. toli*.

Alausa champil Cantor is based on two (dry) specimens which are in fact *Kowala thoracata* Valenciennes. *Clupea champil* Gray is based on a drawing which Cantor (1850) believed to be an "indifferent copy" of one in Hamilton-Buchanan's duplicate (and unpublished) series, labelled by Buchanan "*Clupea champil* B." The drawing can only doubtfully be identified with *Gudusia chapra*.

Some Indian workers have referred to *Gadusia*, but this is incorrect.

†Valenciennes' *Alausa palasah* (1847, p. 433).

DESCRIPTION. Based on 10 fishes, 92–140 mm. standard length from Allahabad (Ganges) and Gowhatty (see list of Study Material).

In percentages of standard length : body depth 32.5–40.0 (see also Figure 13), head length 28.2–30.2 ; snout length 5.0–6.3, eye diameter 7.3–8.5, maxilla length 10.4–12.6 ; operculum, height 13.2–13.6, breadth 6.8–7.3 ; pectoral length 20.2–21.2, pelvic length 11.3–11.7, caudal length 30.0–30.3 ; pre-dorsal distance 48.6–52.5, pre-pelvic distance 49.0–51.7. In relation to standard length, eye diameter and maxilla length show negative allometry.

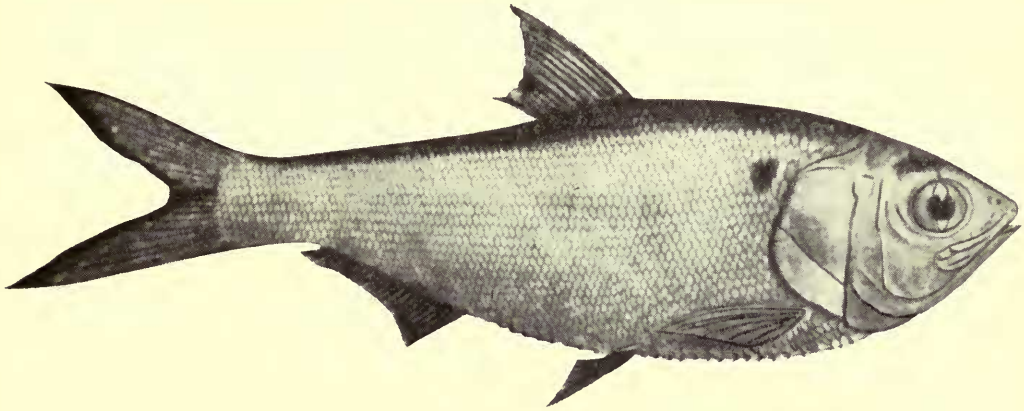


FIG. 11. *Gudusia chapra* (from Day, *Fishes of India*, modified).

Body strongly compressed, its depth greater than head length. Snout less than eye diameter ; pre-orbital length (including eye) just less than post-orbital length. Lower jaw included when mouth shut ; maxilla length four-fifths of pre-orbital length, extending to below eye centre or posterior rim of pupil ; exposed portion without longitudinal ridges or striae ; two supra-maxillae. Pseudobranch attenuated, with groove below, as in *Hilsa ilisha* (Figure 6A). Dorsal without low scaly sheath ; dorsal origin more or less equidistant between snout tip and base of caudal ; pelvic origin below unbranched dorsal rays or just in front, a little nearer to snout tip than to caudal base. Pectorals almost reaching pelvic base ; axillary scale present, one-third to one-quarter length of fin. Pelvic fins half length of pectorals, nearer to pectoral base than to anal origin ; axillary scale present, about one-third length of fin. Anal fin without scaly sheath ; anal origin equidistant between pelvic base and caudal base ; anal base slightly shorter than in *G. variegata*, about three-quarters to four-fifths pectoral length and usually shorter than the distance snout tip to posterior margin of pre-operculum. Caudal fin just less than head length, lower lobe longer than upper.

No teeth. Cutaneous canals of head branching over sub-orbitals, pre-operculum, operculum and onto scales behind head. Adipose eyelid with vertical slit exposing three-quarters of pupil.

Dorsal surface of head covered by skin, but fronto-parietal striae exposed (Figure 1c). Cleithral lobe not prominent, scarcely breaking cleithral outline. Gill fila-

ments of outer hemibranch of first arch half to three-quarters length of those of inner hemibranch. Gillrakers on all arches straight or slightly curved, not curled outwards, about as long as corresponding gill filaments in adults. Bones of opercular series as in Figure 5B, the upper (exposed) margin of the suboperculum rising at a steep angle (to cut dorsal profile before dorsal origin if projected).

Dorsal iv 11-13 (first unbranched ray minute), pelvic i 7, anal (ii) iii 19-22, branchiostegal rays 6. Pre-pelvic scutes 17-19, post-pelvic 10 (11), total 27-29. Scales in lateral series 75-100, 27-34 in transverse series (Regan); exposed edge of scale smooth; minute scales covering caudal except along posterior border. Gillrakers fine and numerous, 200 or more on lower part of first arch (Regan).

The pharyngeal pockets of *G. chapra* have been described by Kapoor (1954, 1957), the morphology of the swim-bladder by Srivastava (1956), and the structure of the alimentary tract by Srivastava (1957).

COLOUR : In alcohol, back brown, flanks silvery or golden, a series of faint black spots along upper flank; caudal edge black.

SIZE : 140 mm. (up to 8 inches—Day, 1889).

DISTRIBUTION : "Freshwaters of rivers and tanks in Sind and throughout India as far south as the Kistna river; absent from the Malabar coast and Madras" (Day, 1889).

Study Material.

1 fish, 85 mm., Cachar (Assam) (1867.2.14.36).

1 fish, 122 mm., Gowhatty (1889.2.1.1952).

1 fish, 102 mm., Lahore (1889.2.1.1953).

1 fish, 76 mm., Goalpara (1889.2.1.1954).

2 fishes, 69-76 mm., Brahmputra (1889.2.1.55-56).

5 fishes, 37-105 mm., Orissa (1889.2.1.57-61).

17 fishes, 46-140 mm., Allahabad, Ganges (1934.10.17.1-10) (7 unregistered).

2 fishes, 41-49 mm., Assam (1963.8.23.1-2).

2 fishes, 99-111 mm., India (1963.8.23.3-4).

(Dry specimens)

1 fish, 148 mm., Ganges (1848.2.1.67).

1 fish, 151 mm., no locality, India House collection (1860.3.19.676).

Gudusia variegata (Day)

Clupea variegata Day, 1869, *Proc. zool. Soc. London* : 623 (type locality, Irrawaddy river, Burma); *Idem*, 1878, *Fishes of India*, pt. 4 : 639, pl. 161, fig. 4; *Idem*, 1889, *Fauna Brit. India, Fishes*, 1 : 375; Vinciguerra, 1890, *Ann. Mus. Civ. Stor. nat. Genova*, (ser. 2) 9 : 350; Lloyd, 1907, *Rec. Ind. Mus.*, 1 : 221; Jenkins, 1910, *Rec. Ind. Mus.*, 5 : 138.

Gudusia variegata : Regan, 1917, *Ann. Mag. nat. Hist.*, (8) 19 : 308; Myers, 1924, *Amer. Mus. Nov.*, No. 150 : 1; Prashad & Mukerji, 1929, *Rec. Ind. Mus.*, 31 (3) : 209; Fowler, 1941, *Bull. U.S. nat. Mus.*, No. 100 : 635.

DESCRIPTION. Based on a single fish, 155 mm. standard length from Bassein (Burma).

In percentages of standard length : body depth 41.6, head length 27.7 ; snout length 5.9, eye diameter 6.4, maxilla length 11.5 ; operculum, height 13.3, breadth 6.9 ; pectoral length 18.2, pelvic length 11.3, caudal length 30.1 ; pre-dorsal distance 49.5, pre-pelvic distance 52.2.

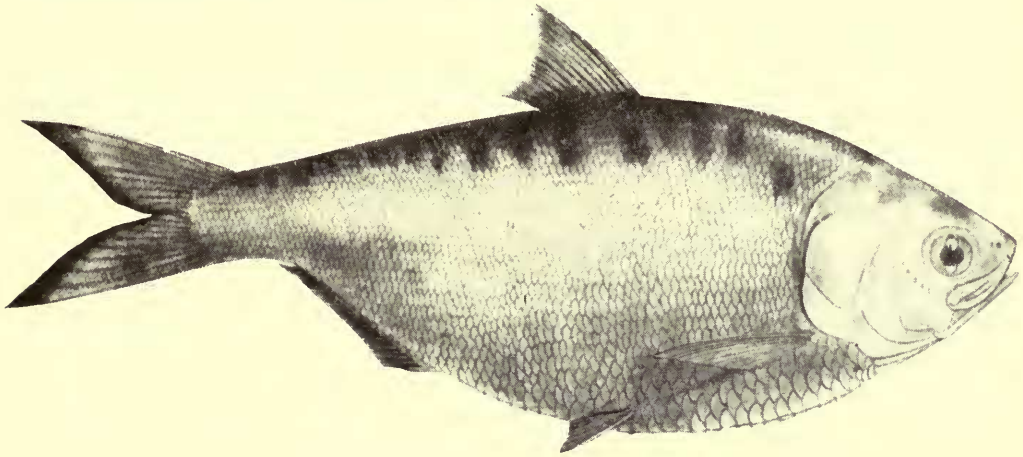


FIG. 12. *Gudusia variegata* (from Day, *Fishes of India*, modified).

Body strongly compressed, its depth one and a half times head length. Snout less than eye diameter ; pre-orbital length (including eye) three-quarters of post-orbital length. Lower jaw included when mouth shut ; maxilla length almost equal to pre-orbital length, extending just beyond eye centre ; exposed portion without longitudinal ridges or striae. Pseudobranch attenuated, with groove below as in *Hilsa ilisha* (Figure 6A). Dorsal with very small scaly sheath ; dorsal origin about equidistant between snout tip and base of caudal ; pelvic origin below unbranched dorsal rays, a little nearer to snout tip than to base of caudal. Pectorals not reaching pelvic base ; axillary scale present, about half length of fin. Pelvic fins a little over half length of pectorals, nearer to pectoral base than to anal origin ; axillary scale present, almost half length of fin. Anal fin with very low scaly sheath ; anal origin equidistant between pelvic base and caudal base ; anal base exceeds pectoral length and exceeds distance snout tip to posterior border of pre-operculum. Caudal fin a little greater than head length, lower lobe longer than upper.

Teeth absent, except minute teeth on tongue. Cutaneous sensory canals of head branching over suborbitals, pre-operculum, operculum and onto scales behind head. Adipose eyelid with vertical slit exposing three-quarters of pupil.

Dorsal surface of head covered by skin, but fronto-parietal striae exposed (see Figure 1c). Cleithral lobe not prominent, scarcely breaking cleithral outline. Gill filaments of outer hemibranch of first arch half to three-quarters length of those of inner hemibranch. Gillrakers on all arches straight or slightly curved, not curled outwards, about as long as corresponding gill filaments. Bones of opercular series as in Figure 5B, the upper (exposed) margin of the sub-operculum rising at a steep

angle (to cut dorsal profile before dorsal origin if projected) ; sub-operculum almost crescentic.

Dorsal iv 12 (first unbranched ray minute), pelvic i 7, anal iii 22, branchiostegal rays 6. Pre-pelvic scutes 19, post-pelvic 11, total 30. Scales in lateral series 90, 32 in transverse series (Regan) ; exposed part of scale with a single prominent vertical striation ; edge of scale pectinated ; minute scales covering caudal except along posterior border.

COLOUR : In alcohol, brown on back, flanks golden, a series of brown spots along upper flank, some expanded vertically, those behind dorsal extending right across back ; dark spot at base of posterior dorsal rays ; caudal tips colourless ("tipped with black"—Day 1869).

SIZE : 155 mm. (7 inches, Day 1869).

DISTRIBUTION : Rivers of Burma.

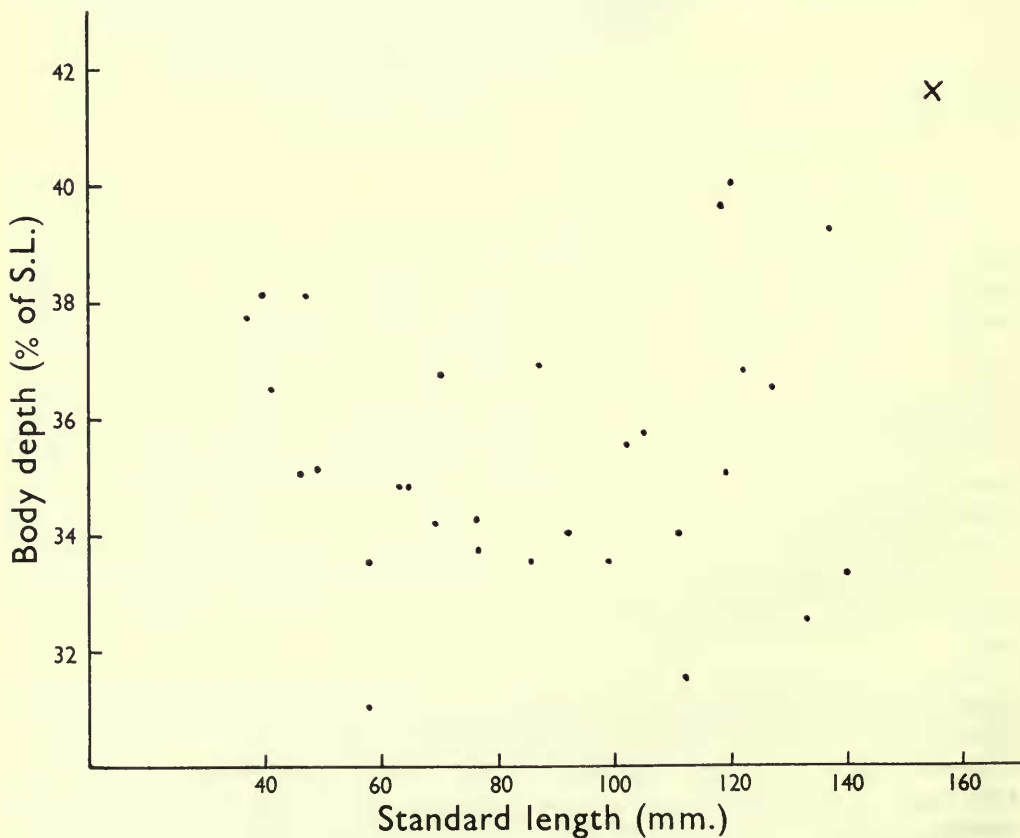


FIG. 13. Body depth as a percentage of standard length, plotted against standard length for species of *Gudusia*.

x *G. variegata* ● *G. chapra*

Relationship to G. chapra.

The differences separating this species from *G. chapra* are small, and it is possible that, when more specimens are available, *G. variegata* will be regarded merely as an eastern form or subspecies of *G. chapra*. The difference in body depth may perhaps be due to allometric growth, since the specimen of *G. variegata* is the largest examined. In Figure 13 body depth as a percentage of standard length is plotted against standard length for 30 specimens of *G. chapra* and 1 of *G. variegata*. The points are rather scattered, but the graph suggests that the body is relatively deeper in fishes below 50 mm. and also in those above 120 mm.

Other differences between *G. variegata* and *G. chapra* are the smooth-edged scales in the latter and perhaps colouration.

THE WEST AFRICAN GENUS *ETHMALOSA*

As noted earlier, the West African genus *Ethmalosa* resembles the Indo-Pacific Alosinae (*Hilsa* and *Gudusia*), and differs from the Atlantic, Mediterranean and New World Alosinae, in two characters, Regan's gillraker character and pelvic fin ray count (8 ; cf 7 or 9). However, the weight attached to these two characters as indicators of probable phyletic relationships must first be viewed in the light of possible zoogeographical relationships.

In general, the clupeoid fauna of West Africa is poor in both species and genera when compared with that of either the New World or the Indo-Pacific. Thus, there are no West African gizzard shads (Dorosomatinae), or round herrings (Dussumieriidae), and only a single engraulid genus, the widespread *Engraulis*, with a single species close to the North Atlantic *E. encrasicolus* (Whitehead 1964b). In the subfamily Clupeinae, records of *Sardina pilchardus* have probably been based on one or two stray fishes from the North Atlantic. *Sardinella*, however, with two species, *S. aurita* Valenciennes and *S. maderensis* (Lowe), is principally an Indo-Pacific genus. *S. maderensis* (for which *S. eba* [Valenciennes], *S. granigera* Valenciennes and *S. cameronensis* Regan are probably synonyms) occurs only off the West African coast and in the Mediterranean, but *S. aurita* is found along the Atlantic coast of America, in the Mediterranean, and also in the Western Pacific (Japan, Philippines). *S. aurita* is, however, replaced in the Indian Ocean by *S. longiceps* Valenciennes. *Harengula*, a Western Atlantic genus, is not represented in West Africa ; *H. rouxi* Poll is a species of *Sardinella* (Whitehead 1964a). The subfamily Pellonulinae shares no genera with the Indo-Pacific.

Finally, in the subfamily Pristigasterinae, the genus *Ilisha* is shared both with the Indo-Pacific and with the Western Atlantic. But Tucker (1954) believed the West African species, *I. africana* (Bloch), to be more closely allied to the species and genera of the Atlantic coast of South America than to any Indo-Pacific form. He felt that there might one day be a case for recognising the distinctness of the West African *I. africana* from the Indo-Pacific forms by the creation of a new subgenus.

Thus, only two West African clupeid genera are shared with the Indo-Pacific. But they are also the only two Western Atlantic clupeid genera which are found in West Africa ; and at species level both show closer links with the Western Atlantic

than with the Indian Ocean. On zoogeographic grounds, therefore, *Ethmalosa* would be expected to show less affinity with the Indo-Pacific than with the New World genera.

Against this argument, there is further morphological evidence linking *Ethmalosa* with the Indo-Pacific Alosinae. The fronto-parietal striation pattern is identical to that found in *Hilsa kelee* (but it also resembles that in *Brevoortia*). Perhaps more significant, the rather characteristic gillrakers on the upper parts of all arches and the lower parts of the third and fourth arches in *Ethmalosa* may well represent merely an extreme form of the curled gillrakers found in *Hilsa kelee*. The pseudo-branch in *Ethmalosa* also resembles that of *H. kelee*. On the other hand, the maxilla in *Ethmalosa* is smooth (but ridged in *Brevoortia*) and the cleithral lobe is little developed (as in *Brevoortia*, *Alosa*).

On present evidence therefore, the question must remain open. *Ethmalosa* may have been derived from the Western Atlantic, or from the Indian Ocean, or it might represent an independent relict of a once widespread alosinid fauna. Until this problem can be solved, a tribal division in the Alosinae would be unrealistic.

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It is a pleasure to record my thanks to Dr. M. Boesman, of the Rijksmuseum van Natuurlijke Historie (Leiden) for his help in the problem of *Hilsa macrura*. The manuscript was read by Dr. P. H. Greenwood, to whom go my sincere thanks for suggestions and criticisms. Finally, I must express my gratitude to Dr. M. Blanc of the Museum National d'Histoire Naturelle, Paris, who so willingly lent me Valenciennes' specimens and other material, and kindly undertook the measurements on type specimens of *H. toli*.

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